Strategic Planning for Ontario Fisheries

Policy Development

Partitioning Yields Estimated from the Morphoedaphic Index into Individual Species Yields

Report of SPOF
Working Group Number Twelve

March 1982

Ontario
Ministry of Natural Resources

Hon. Alan W. Pope
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EXECUTIVE SUMMARY

Establishing guidelines for the rational harvest of a freshwater fishery as complex as Ontario's, is a formidable task. Fortunately, recent conceptual insights gained in fishery science allow us to advance beyond the management of a single species and develop guidelines for managing certain multispecies fisheries.

The purpose for developing these guidelines is to partition the overall potential yield derived from the morphoedaphic index into allowable yields for several economically important species without jeopardizing the integrity of the fish community.

This pioneer approach to managing fish communities was made possible by development of the MEI to predict potential yields and by recent international symposia devoted to synthesizing trend-through-time data (e.g. SCOL, PERCIS, SLIS).

The respective commercial and angling yields as a percentage of the potential yield ($\hat{Y}$) where $\hat{Y}$ (kg ha^{-1}) = 1.4 $(MEI)^{0.45}$ are recommended for the following species: Brook trout (N/A, 25); Lake trout (25, 25); Lake whitefish (24, 24); Northern pike (10-20, 25); Smallmouth bass (N/A, 17-50); Walleye (20, 32) and Yellow perch (?, 13). Here N/A indicates that the guidelines are not applicable.

Managers must use caution in determining the suitability of these guidelines for their fishery. The guidelines are most appropriate for regulating harvests of natural populations in lakes either lacking historical data sets,or large lakes supporting primarily commercial fisheries. They should be useful in planning initial harvests or regulating those commercial

harvests where methods of capture are heavily impacting the reproductive potential of the stock. The guidelines are not appropriate to artificial fisheries supported by plantings. There is also concern as to whether these guidelines are appropriate for certain percid fisheries, especially for sport fisheries on high yield walleye lakes, where yields have exceeded the guidelines for many years. When there are ample historical fishery statistics available, managers should utilize this additional stocks information for regulating harvests. If the harvests exceed the guidelines the manager should be especially alert to monitor those criteria which indicate whether the stock is in danger of being overexploited and subsequent collapse, or whether an undesirable alteration of the structure of the fish community is likely to occur. Criteria for determining whether a stock is being overexploited are being developed by SPOF Working Group 15.

Finally, users of the guidelines should realize that the present state-of-the-art in fishery science is limited by inadequacies of the data and the dearth of conceptual insights as to how communities respond to disturbances. Our present empirically derived yield models reflect the manner our culture has historically impacted these fish communities. These models are not the result of carefully designed experiments and consequently provide less than ideal insights as to how these communities can be optimally harvested as society's preferences change. Through research and collection of more accurate and comprehensive, bait, commercial, subsistence, and domestic harvest statistics; creel census; and reliable province-wide angler surveys these guidelines will be improved. There is increasing evidence that the method of harvesting, nature of the ecosystem (open vs. closed), community structure, and the availability of energy and nutrients are important factors

in determining sustainable yields. Therefore, we have suggested some approaches to test the validity of these guidelines and for making the necessary modifications as appropriate information becomes available. These guidelines are therefore of interim value and will probably need to be revised in 3-5 years.

INTRODUCTION

Objective

The original purpose of the study which led to the development of the morphoedaphic index was "... to provide basic edaphic information on small, medium and large Ontario lakes with accompanying suggestions as to how this information in the latter two categories may best be utilized in estimating fish production when combined with morphometric data. Because of the vast area of remote lake country in Ontario, this method seems more practical than the more intensive fisheries and limnological studies, although the latter are essential for complete understanding of the situation" (Ryder 1964a). As a result, the morphoedaphic index (MEI) equation was formulated to predict the potential fish yield for a lake from a minimum of information, namely the total dissolved solids (TDS) concentration and mean depth ($\bar{Z}$) of the lake. The objective of this report by SPOF Working Group 12 was to develop policy guidelines for dividing this total potential yield into allowable yields for individual species. The species yield estimates are analagous to the SPOF Report #4 (1979) term "allowable yield" in that the recommended level of harvest allows for brood stock maintenance and stock rehabilitation without altering fish community structure.

Highlights in the development of the MEI concept

Rawson (1952, 1955) was probably the first to give a clear demonstration of the relation between fish production and lake morphometry. On plotting annual commercial fish landings (Y) against mean depths for 13

large North American lakes, he obtained the following equation: $Y = 30.255\ (\bar{Z})^{-0.7029} + 0.5$, where the yield (Y) is in lbs $acre^{-1}$ and the mean depth ($\bar{Z}$) is in ft. The fraction of the lake volume receiving sufficient sunlight to support photosynthesis and having temperatures conducive to optimal metabolic rates is smaller for a deep lake than for a shallow one. Moreover, deep lakes may stratify strongly with respect to temperature and chemistry during the summer and, under such circumstances, nutrients may become tied up in the deeper layers of water. Conversely, recycling of nutrients and energy is likely to be more efficient in shallow less strongly stratified lakes.

Moyle (1956) found that commercial fish landings from Minnesota lakes were positively correlated with the total phosphorus, total nitrogen and total alkalinity of the lake waters, and that these factors were in turn related to the geology of the watersheds. A similar relation between fish yields, water chemistry and geology has been described by Ryder (1964a,b) for Ontario lakes. Lakes located in the sparse soils of the Precambrian Shield tend to be oligotrophic, whereas those in deep glacial overburden and limestone bedrock are usually mesotrophic or eutrophic.

On plotting annual commercial catches from 23 moderately to heavily fished Canadian lakes against the ratio of total dissolved solids to mean depth, Ryder (1965) obtained the regression line: $\hat{Y} = 2.094\ (TDS/\bar{Z})^{0.4461}$, where $\hat{Y}$ is the yield of fish in lbs $acre^{-1}yr^{-1}$, TDS the total dissolved solids in mg l^{-1} and $\bar{Z}$ the mean depth in ft. Because the ratio $TDS/\bar{Z}$ combines a measure of the nutrients leached into the lake from the soils on the watershed (TDS) with an indicator of the form of the lake basin ($\bar{Z}$), Ryder termed it the morphoedaphic index. The metric equivalent of Ryder's

formula, obtained by converting his original data to metric units and refitting the line is: $\hat{Y} = 1.4\ (TDS/\bar{Z})^{0.45}$ or $Y = 1.4\ (MEI)^{0.45}$ where $\hat{Y}$ is in kg $ha^{-1}\ yr^{-1}$, TDS in mg l^{-1} (= ppm) and $\bar{Z}$ in m.[1] This form is used for determining potential yields throughout this report but references are made to alternate formulae intended to allow for differences in latitude and solar energy input.

Ryder also cited a group of 11 lakes which appear to lie on a line parallel to, but much lower than, $\hat{Y} = 1.4\ (MEI)^{0.45}$, and noted that these were relatively lightly exploited because of their remoteness or other conditions. Hence, he recognized the role of effort as well as MEI in determining fish yields. However, he did not deal further with this factor probably because of the difficulty in getting reliable data on commercial fishing effort.

The MEI model has subsequently been fitted to data from 103 reservoirs in the United States (Jenkins and Morais 1971), 30 or more African lakes (Henderson *et al.* 1973; Henderson and Welcomme 1974), and some lakes in northern Finland (Ryder *et al.* 1974), indicating the universality of the concept. The latter authors also found that fish yields depended on the geographic location of the lake as well as its MEI. The yield for a given MEI is higher for a tropical lake than for a northern one, owing to the greater insolation of the former. Recent studies of variations in the growth rate of walleye over its north-south range suggest that isopleths of growing

---

[1] The conversion to metric can also be made by multiplying the intercept, 2.094, of the original equation by the factor $0.6593 = 1.12(0.3048)^{0.45}$, where 1 lb $acre^{-1}\ yr^{-1}$ = 1.12 kg $ha^{-1}\ yr^{-1}$ and 1 ft = 0.3048 m.

day degrees above 5C may be an even better indicator of the input and utilization of solar energy than degrees of latitude (P. Colby, pers. comm.).

The reservoirs studied by Jenkins and Morais (1971) afforded a wider range of MEIs than Ryder's 23 lakes, and they found that the line relating yield to MEI took the form:

$$Y = {}_{10}\left[0.0765 + 1.725\ (\text{LogMEI}) - 0.477\ (\text{LogMEI})^2\right]$$

where Y was the catch of sport fish in kg ha^{-1} yr^{-1}. Although a polynomial fit to Ryder's data improves the correlation slightly, the equation $\hat{Y} = 1.4\ (\text{MEI})^{0.45}$ seems adequate for our present purpose.

Regressions of yield on MEI for various globally distributed sets of lakes indicate that the slope of the line is relatively constant but the intercept changes according to varying energy inputs in different climatic regions (Ryder *et al.* 1974). Accordingly, SPOF Working Group 4 (Ontario Fish Yield Estimates) recognized 5 climatic regions or "potential fish yield zones" and suggested an appropriate MEI equation for each. In metric form these are:

1) Southern agricultural zone: $\hat{Y} = 2.31(\text{MEI})^{0.446}$
2) Northern Great Lakes-St. Lawrence watershed: $\hat{Y} = 1.38(\text{MEI})^{0.446}$
3) Southern James-Hudson Bay watershed: $\hat{Y} = 0.66(\text{MEI})^{0.446}$
4) Winnipeg-Nelson watershed: $\hat{Y} = 1.38(\text{MEI})^{0.446}$, and
5) Hudson Bay lowlands; no formula given, $\hat{Y}$ assumed to be 1.12 kg ha^{-1} yr^{-1}.

For the algebra involved in converting from English to metric units and square-root approximations see the report of SPOF Working Group 10 (Guidelines for District Fisheries Management Plans). It should be realized, however, that these formulae depend heavily on subjective judgements.

A more objective approach to incorporating the solar energy into the MEI model is offered in a recent study by Schlessinger and Regier

(1982). From a data set of 43 globally distributed and intensively exploited commercial fisheries, for which the reported yield was assumed to be a close approximation to the maximum sustainable yield for the lake, they obtained the regression line: $\log_{10}Y = 0.05(TEMP) + 0.280(\log_{10}MEI) + 0.236$, where Y is the estimated potential (or maximum sustainable) yield for the fish community in kg ha^{-1} yr^{-1}, TEMP the mean annual air temperature in the vicinity of the lake in ^{o}C, and the MEI is in metric units. The r^2 values indicate that differences in TEMP accounted for 74% of the variability in potential yield while differences in MEI explained 7-9%. According to this formula a lake with an MEI of 5 in the vicinity of Sault Ste. Marie (TEMP = $3.8^{o}C$) would have a potential yield of 4.2 kg ha^{-1} yr^{-1}, whereas a lake with the same MEI in the Lindsay District (TEMP = $6.1^{o}C$) would have a potential yield of 5.4 kg ha^{-1} yr^{-1}.

For the present, the fisheries manager should select the formula most appropriate to his or her part of the province. It is expected that current research by Colby (MNR) and Regier and associates (University of Toronto) will result in more objective and precise models for estimating potential fish yields within the next few years.

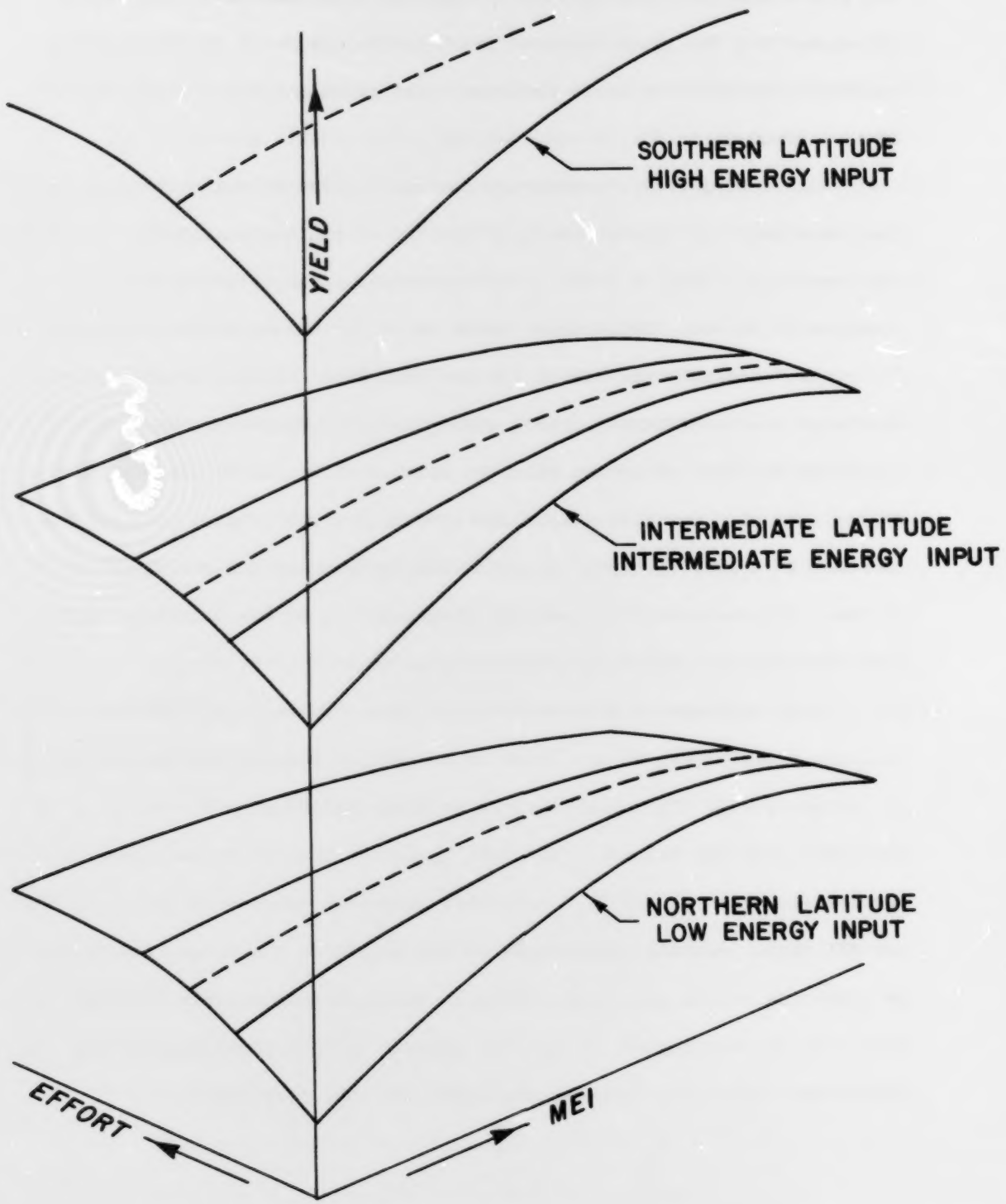
Jenkins and Morais (1971), Henderson and Welcomme (1974), Adams and Olver (1977), and McCombie (1981) also found that fish yields were strongly correlated with the effort expended by commercial fishermen or anglers and proposed models to incorporate effort and MEI. Regression analyses on creel census data from 42 lakes in the Minden and Bracebridge Districts and additional data from some Kawartha lakes, some Sault Ste. Marie District lakes and one large multibasin Minnesota lake gave the line:
$\log_e Y = 0.295(\log_e MEI) - 0.006(\log_e MEI)^2 + 0.654(\log_e E) - 1.717$, where Y is the potential yield in kg ha^{-1} yr^{-1}, E is the effort in angler-hours ha^{-1} yr^{-1}, and the MEI is in metric units (McCombie 1981).

Ryder assumed that, since the fisheries in the lakes he selected had been carried on for many years under moderate to intensive pressure, the catches indicated "continuing availability of fish" and he called the value estimated from the MEI formula the "potential" production or yield. Hence, this term is used in the present report. However, following the period from which Ryder drew his data, several of these fisheries deteriorated as a result of increasingly heavy fishing and other stresses (see reviews by Smith, Keleher, Lawrie and Rahrer, Berst and Spangler, Hartman, Christie, Wells and McLain in the SCOL Symposium 1972). It has been suggested, therefore, that the potential production or yield estimated from the MEI formula is analogous to the maximum sustained yield (MSY) (Matuszek 1978) or, more precisely, the community maximum sustained yield (MSY_c) (McCombie 1981)

Although the work of Rawson, Moyle and Ryder was based on commercial fish landings, many of the species taken commercially were also sport fish. Hence, the MEI formula would appear applicable for estimating potential yields of both commercial and game species although it may be somewhat less appropriate in estimating angling yields. It is not suitable for estimating yields of small species such as minnows, troutperch, darter, etc. or suckers, since these were not included in the original MEI derivation. We assume however, that yields of these fish can be accommodated in a revised MEI model when data are available.

The relations between fish yield, MEI, fishing effort and energy input described above are summarized schematically in Fig. 1. The interrupted line on each regression surface represents the potential yield (or community sustained yield). The solid lines above or below the interrupted line on each surface represent yields from lakes which are over or underexploited, respectively. Other factors which may affect observed and potential yields,

Figure 1. Schematic presentation of the relations between fish yields, MEI, effort and energy input.


YIELD
SOUTHERN LATITUDE
HIGH ENERGY INPUT
INTERMEDIATE LATITUDE
INTERMEDIATE ENERGY INPUT
NORTHERN LATITUDE
LOW ENERGY INPUT
EFFORT
MEI

but which are not included in this illustration, are species composition of the fish community, availability of food and fluctuations in year class strength. For any given value of the MEI, the yield may be higher for a community dominated by early maturing, fast growing species than for one of slow growing, late maturing species.

As fishing effort increases, the yield taken from the fish community increases until it approaches the potential or maximum sustainable yield for the community. Then it tends to become constant (asymptotic) with further increase in effort. This would appear to be the situation with the Lake Erie fisheries. However, the yields for the individual species which make up the community show a different trend, rising to their respective maxima as effort increases and then declining when the rate of fish removal exceeds the rate of replacement. One reason that the community yield remains more or less constant at higher levels of exploitation is that species having shorter turnover of generations replace the longer lived, slower maturing species. Also more fecund species may replace less fecund.

With increase in MEI the community yield rises to a maximum and then declines again. Few, if any, game or commercial species are adapted to live at extremely high TDS concentrations or very shallow mean depths (i.e. at extremely high MEI values). But here again there tends to be a succession of species (Colby *et al.* 1972). Salmonids seem best adapted to the lower end of the MEI range, esocids and percids to the middle of the range, and centrarcids or cyprinids to the upper end, although there is considerable overlap. In this case the sorting out of species appears to be a physiological and perhaps behavioural response, to water chemistry and lake morphometry.

Need for a margin of safety

Larkin (1977) has recently argued that, although the maximum sustained yield is a useful first approximation of the potential fish production for a body of water, it is unwise to try to exploit the fishery at that level. For one thing, a fishing effort sufficient to take any MSY_c made up of several species of fish may actually have a greater impact on some of the species than others. Even in single species fisheries, some stocks may be more affected by the fishing pressure than others. Exploitation to full MSY_c also fails to provide any margin of safety in the event of weak year classes (Doubleday 1976; Sissenwine 1978). Also, SPOF Report #4 (1979) pointed out that "since no socio-economic considerations such as access, marketability, contaminants or angler preferences are introduced into the potential yield estimate, it is clearly not a target level of fish yield for the forseeable future." Therefore, to provide a margin of safety, it is recommended that the total yield of all species should be a fraction of the potential yield or MSY_c, and the yield for an individual species a fraction of the total yield. Guidelines for selecting these fractions and the exceptions are described in this report.

METHODS AND SOURCES OF DATA

Procedures for partitioning MEI potential yield

At least four different methods for determining the sustainable yields of individual fish species have been described in the literature. The rationale for setting allowable limits to walleye catches suggested by Carlander (1977) in the PERCIS Symposium has much to recommend it from a standpoint of logic, but has limited application at present owing to the scarcity of annual production figures. He found that annual production in 4 walleye lakes ranged from 1.2 to 4.1 kg ha^{-1} yr^{-1} and pointed out that the sustained yield cannot exceed the annual production if the fishery is to survive. Taking somewhat less than the annual production is analogous to living on interest from one's investments, whereas taking more is comparable to drawing on the principal. However, in Escanaba Lake (Kempinger and Carline 1977) the long term mean walleye yield (9 kg ha^{-1} yr^{-1}) exceeded annual production estimates for the period 1966-69 of 4.9 to 7.6 kg ha^{-1} yr^{-1} , indicating that the methodologies currently available for assessing production require further research.

Because sustainable yields of short-lived, early-maturing fish species are probably greater than those for long-lived, slow-maturing species, Ryder (pers. comm.) recommends the procedure adopted by Regier *et al.* (1971), Ryder and Henderson (1975) and Ryder (1978) in calculating potential yields for tropical reservoirs. They used the Gulland (1970) equation: $Y = kMB$, where Y is the estimated total fish yield on a long-term basis; k is a constant such that $0.3<k<0.5$ (typically 0.4); M is the community mortality coefficient based on individual species mortality coefficients weighted according to their proportionality in the total harvest; and B is the standing crop of the fish community,expressed as biomass,prior to fishing. Where data on standing crops of fish are not available, one might use the procedure

adopted by Ryder and Henderson (1975) to calculate yields for the Nasser Reservoir. In that case they applied the particle size hypothesis of Sheldon *et al.* (1972) which states that, although the size of organisms in the various trophic levels differ greatly, the standing crop is about the same in each level. Accordingly they substituted the standing crop of zooplankton, which was available from another study of the reservoir, for the standing crop of fish. Alternatively one might estimate the standing stock of fish from a regression of standing stocks of fish on MEI similar to that obtained by Jenkins (1967) for United States reservoir fisheries. Unfortunately, there does not seem to be sufficient information available at present on standing crops of either fish or zooplankton in Ontario lakes to facilitate application of the Gulland model.

On the other hand, there is much information available on the size and species composition of both sport and commercial fisheries in Ontario lakes which lends itself to the method described by Adams and Olver (1977) in the PERCIS Symposium. This entails selecting a set of fisheries (lakes) which have apparently withstood moderate to heavy fishing for several years and taking the averages of the species yield to total yield and species yield to potential yield, i.e. Y_s/Y_t and $Y_s/\hat{Y}$. The latter ratio, expressed as a percentage, is taken as the guideline or recommended allowable yield for each species dealt with in this report. The measure of fishing effort used here to select the set of moderately to heavily fished lakes is the ratio of the total yield of all species to the potential yield, which Adams and Olver termed the relative yield index (RYI = $Y_t/\hat{Y}$). We feel that this index provides a useful means of making lake-to-lake comparisons of what the fishermen are taking from the lake relative to what the lake can produce.

Since Adams and Olver were faced with the classic problem of the lack of adequate, direct measures of fishing effort in commercial fisheries, they

assumed the RYI would reflect the lake-to-lake differences in effort and vulnerability of stocks, as well as differences in MEI. If this asumption is a valid one, then one would expect to find a significant correlation between the RYI and effort stated in some direct measure, such as angler-hours (Fig.2). Even higher correlation coefficients were found in an analysis of data from West Patricia District fisheries when the lakes were divided into two size groups and effort was measured in angler days (P. Ryan, pers. comm.). For lakes of area less than 1,000 ha : RYI = 0.373 + 1.356(E) and r = 0.94 with 66 d.f. For lakes of area greater than 1,000 ha: RYI = 0.381 + 1.588(E) and r = 0.89 with 60 d.f. In this case the relative yield index was defined as : $RYI = \frac{\text{observed yield}}{\text{40\% of potential yield}}$ where 40% of potential yield was considered to be the fraction of the yield estimated from Ryder's MEI formula which could be taken in the form of pike and walleye.

As a supplemental approach to determining the allowable yield for lake trout we used the model described by McCombie (1981) in the Lakeshore Capacity Study. A plot of mean age of lake trout caught and retained by anglers against the ratio of lake trout yield to potential yield of all species for 11 Ontario lakes and one in Minnesota gave the die-away curve shown in Fig. 3. The lake trout sport fishery on Lake Opeongo, Algonquin Park, has remained stable for 40 years under an average RYI of 16%, and in Lake Joseph, Muskoka area, where the lake trout fishery still appears to be satisfactory, the RYI is about 40%. However, as the RYI exceeds 40%, the mean age of lake trout caught approaches the mean age at first maturity (i.e. 6-7 years), suggesting that spawning stocks may be seriously reduced. Trout Lake, Minnesota, is an example of a lake which is considered to have been greatly overfished (Schumacher 1961).

Note that the underlying purpose of this method is to determine whether taking an increasing proportion of the potential yield in the form of a particular species will change the demographic characteristics of the catch of that species and, if so, at what point might the change become critical to spawning stocks. It is hoped that it can be tested with additional data from other trout fisheries and for other species in future. The model would be greatly improved, of course, if the mean age of the fish population derived from experimental netting were substituted for the mean age of catch, since the latter may be biased by the gear and/or method of fishing.

Selection of data sets and species

Data are presented for the sport fisheries in 68 Ontario lakes, four Minnesota lakes and one California lake (Tables 1 and 2). These were selected because they involved a variety of species of interest in the province and because reasonably reliable creel census records were available. Species considered are the lake trout, northern pike, smallmouth bass, walleye, and yellow perch. Some comment is also made on brook trout and lake whitefish. Although rainbow trout, muskellunge, lake herring, largemouth bass, panfish, and bullheads are also taken by anglers from some of these lakes, there was not sufficient information on these species to prepare guideline yield estimates.

Tables 3 and 4 give data for 22 representative commercial fisheries for lake whitefish, walleye and pike, taken from Adams and Olver (PERCIS Symposium 1977) and for 9 commercial lake trout fisheries, taken from other sources as indicated. While lake trout were also taken in some of the whitefish, walleye and pike lakes, the catch data for lake trout from those fisheries were not used here because they were not a target species and catches were

Figure 2. Regression of relative yield index (total catch of all species/ potential yield from MEI) and effort in angler-hours ha^{-1} yr^{-1}. The equation for the line is: RYI = 0.199 + 0.0301 (Effort), r = 0.737 with 37 d.f. and $P<0.01$. Based on data from Bracebridge and Minden District lakes (McCombie 1981).

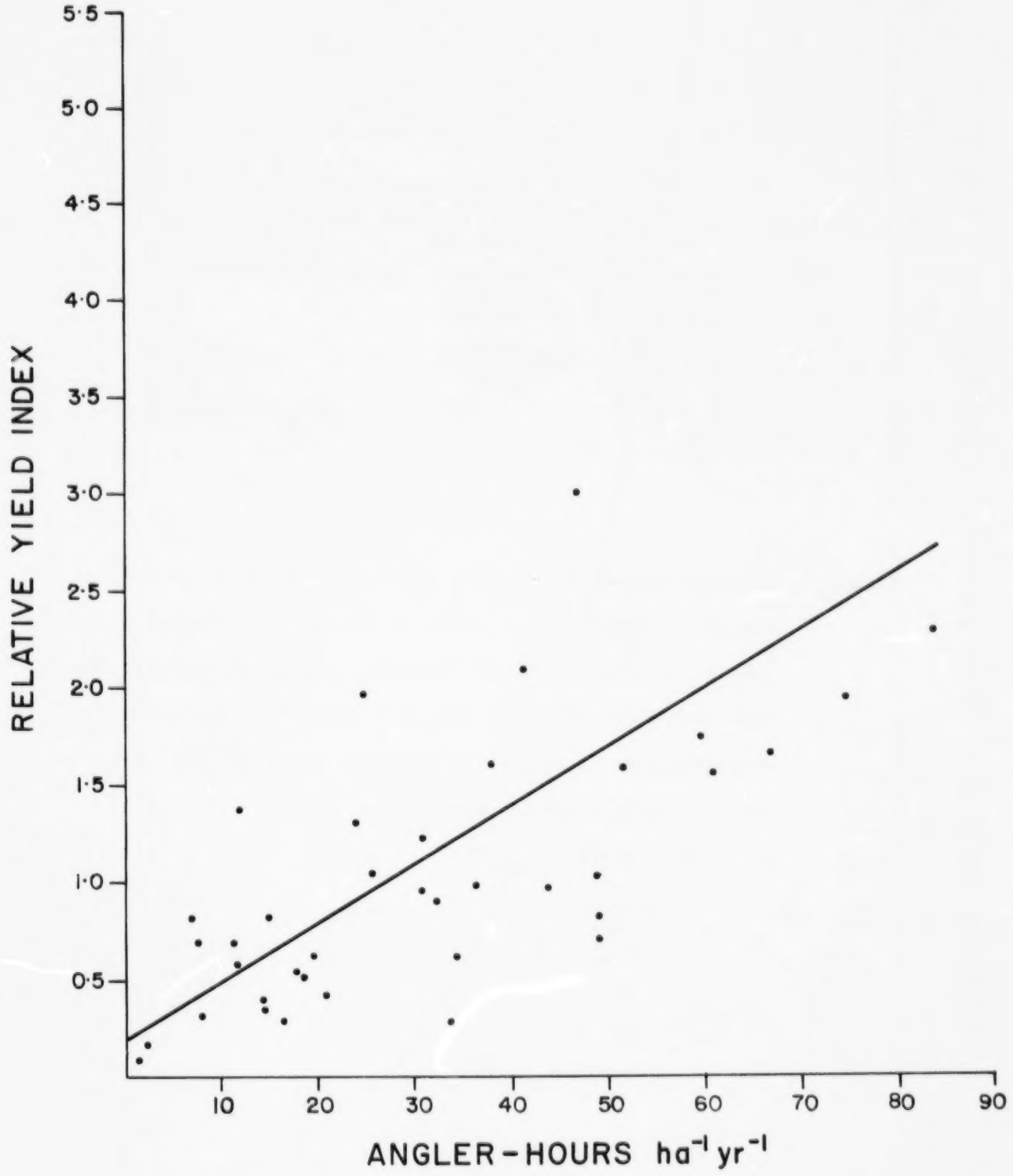
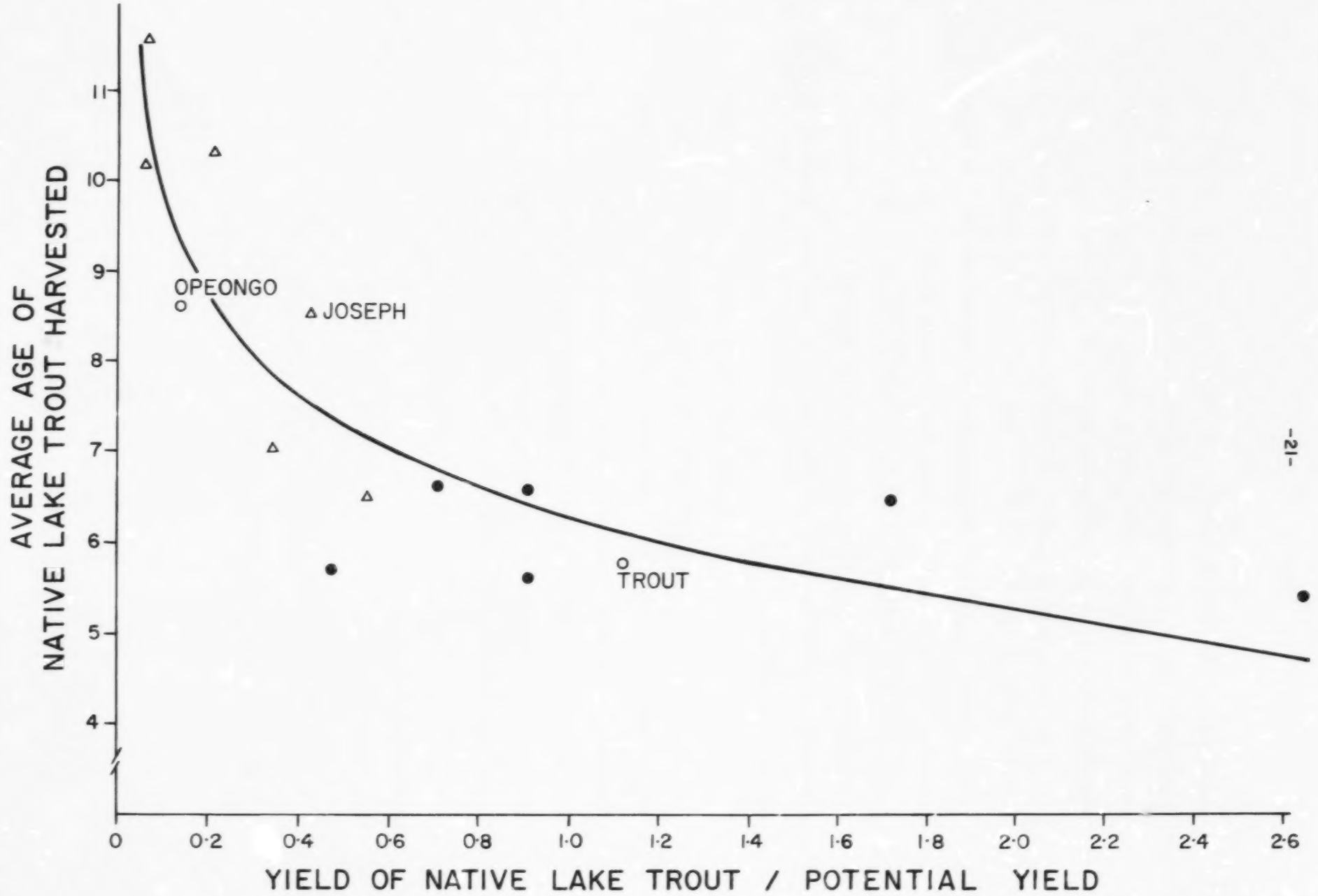

RELATIVE YIELD INDEX
5·5
5·0
4·5
4·0
3·5
3·0
2·5
2·0
1·5
1·0
0·5
10
20
30
40
50
60
70
80
90
ANGLER-HOURS ha⁻¹ yr⁻¹

Figure 3. Relation between the mean age of lake trout caught in some Lakeshore Capacity Study lakes and the ratio: yield of native lake trout/potential yield from MEI. The Opeongo fishery has been stable for 40 years; the Trout Lake, Minnesota fishery is overexploited. Δ Bracebridge district lakes; ● Minden district lakes. The equation for the line is:

$A = 6.293 - 1.464 \ (\text{Log}_e Y_s/\hat{Y})$.


AVERAGE AGE OF
NATIVE LAKE TROUT HARVESTED
11
10
9
8
7
6
5
4
OPEONGO
JOSEPH
TROUT
0
0·2
0·4
0·6
0·8
1·0
1·2
1·4
1·6
1·8
2·0
2·2
2·4
2·6
YIELD OF NATIVE LAKE TROUT / POTENTIAL YIELD

incidental to the catch of other species and, therefore, felt to be unsuitable. Data for the commercial fisheries were reported on an annual basis and were not broken down by season. In general, commercial fishing is confined to the open water months.

For the commercial whitefish, pike and walleye fisheries, the relative yield index (RYI) was 48% to 90% and for the commercial lake trout fisheries, it was 21% to 141%. For the sport fisheries considered here, the fishing intensity, as measured by the relative yield index, ranged from 7% to 270%. We would have liked to have chosen only fisheries with RYI = 50-100% for all the data sets, but scarcity of information obliged us to widen the range for the commercial lake trout fisheries and the sport fisheries.

In addition to the above data sets, three special sets provided by the Lakeshore Capacity Study (McCombie 1981), L. Thurston (pers. comm.) and J. Chevalier (pers. comm.) were drawn upon to illustrate the relations between: (1) RYI and effort measured in angler-hours; (2) removal of bullheads and increase in numbers of largemouth bass caught; and (3) the percentage of the harvest represented by a single species, namely lake trout, and the number of species present in the lake.

Standardization of the TDS data

See Appendix 2

Table 1. Morphometric, total dissolved solids (TDS), length of fishing records and yield data for the sport fisheries used here as a basis for partitioning the potential yield ($\hat{Y}$) by species, where $\hat{Y} = 1.4(MEI)^{0.45}$.

Lake name	Area (ha)	Mean depth (m)	TDS ($mg\ell^{-1}$)	MEI	Length of record	Yields in kg $ha^{-1}yr^{-1}$								
						Lake trout	N. pike	S.M. bass	Wall-eye	Yellow perch	Total (Y_t)	Potential ($\hat{Y}$)	RYI% ($100Y/\hat{Y}$)	Sources of data
Tahoe (Calif.)	49937	313	62	0.20	3Y	0.27					0.27	0.67	40	Cordone & Franz 1966
Chiblow-Denman	2725	23.9	16	0.67	10S***	0.78		0.14			0.92	1.17	79	Chevalier, pers. comm.
Flack	934	21.5	17	0.79	9S***	1.24					1.24	1.26	98	Chevalier, pers. comm.
Kawagama	2819	21.8	19	0.87	4S3W	0.42		0.22		0.22	0.87	1.32	66	LSCS
Joseph	4973	25.3	25	0.99	4S3W	0.33		0.15			0.84	1.39	60	LSCS
Redstone	1193	21.9	22	1.00	3S3W	1.39				0.01	1.54	1.40	110	LSCS
Lake of Bays (Bracebridge Dist.)	7053	22.3	23	1.03	4S3W	0.04		0.09		0.03	0.21	1.42	15	LSCS
Rosseau	5827	25.5	29	1.14	4S3W	0.05		0.02		0.07	0.45	1.48	30	LSCS
Little Quirke	389	13.5	17	1.26	3W*	0.33					0.33	1.55	21	Chevalier, pers. comm.
Semiwite	304	13.7	18	1.31	9S***	0.76					0.76	1.58	48	Chevalier, pers. comm.
Clearwater (Minn.)	537	12.8	18	1.37	3Y	0.25					0.25	1.61	16	Schumacher 1961
Darragh	182	14.7	21	1.43	2W*	0.82					0.82	1.64	50	Chevalier, pers. comm.
Bone	123	8.5	13	1.53	9W*	1.97					1.97	1.69	116	Chevalier, pers. comm.
Opeongo	5860	14.6	23	1.57	36S***	0.33					0.33	1.72	19	Martin & Fry 1973
Happy Isle	536	13.0	23	1.77	19S***	0.28					0.28	1.81	15	Martin 1966
Mississagua	588	17.7	34	1.92	2S1W	0.30		0.50		0.04	0.93	1.88	49	LSCS
Haliburton	998	17.4	35	2.01	4S#	0.30		0.27			0.62	1.92	32	LSCS
Bernard	2185	15.8	32	2.02	4S3W	0.45		0.42		0.20	1.23	1.92	64	LSCS
Temagami	21594	18.2	37	2.03	2S5W	0.29		0.02	0.09		0.46	1.93	24	Duckworth 1979, Koski 1976a,b; 1978
Jimchrist	58	8.8	19	2.16	9S***	1.62					1.62	1.98	82	Chevalier, pers. comm.
Lavieille	2426	14.4	33	2.29	2S***	0.39					0.57	2.03	28	Hicks, pers. comm.
Drag	1003	18.0	42	2.33	2S2W	0.21		0.37		0.04	0.68	2.05	32	LSCS
Pevensey	155	9.1	22	2.42	1S2W	0.63				1.03	1.67	2.08	80	LSCS
Gull	995	16.5	41	2.48	4S3W	1.78		0.03		0.03	1.96	2.11	93	LSCS
Mountain	319	13.4	36	2.69	1S1W			0.71			1.74	2.18	80	LSCS
Pickerel (Bracebridge Dist.)	513	8.6	24	2.79	4S**		1.33	0.24	1.00	0.02	2.59	2.22	116	LSCS
Sturgeon (Ignace Dist.)	21413	13.6	38	2.79	1S	0.30	0.08		0.04		0.42	2.22	19	Ryan, pers. comm.
Merchant	389	8.9	27	3.03	19S***	0.66					0.66	2.30	29	Martin 1966

Table 1. (Continued)

Lake name	Area (ha)	Mean depth (m)	TDS ($mg\ell^{-1}$)	MEI	Length of record	Yields in kg $ha^{-1}yr^{-1}$								Sources of data
						Lake trout	N. pike	S.M. bass	Wall -eye	Yellow perch	Total (Y_t)	Poten -tial ($\hat{Y}$)	RYI% ($100Y/\hat{Y}$)	
Red 2 & 4	12541	12.5	38	3.04	1S#		0.54		0.92		1.46	2.31	63	Ryan, pers. comm.
Spring	70	22.2	70	3.15	3Y	0.60					0.60	2.35	25	Chevalier, pers. comm.
Red 1	4486	12.1	39	3.21	1S#	0.21	0.59		0.28		1.08	2.37	46	Ryan, pers. comm.
Northern Light	6866	8.4	27	3.21	1S##	0.07	0.02	0.05	0.25		0.55	2.37	23	Ryan, pers. comm.
Eagle (Bracebridge Dist.)	991	6.1	21	3.44	2S***		0.03	0.92	0.01	0.44	1.41	2.44	58	LSCS
Kashagawigamog	778	13.0	45	3.46	4S2W	0.11		0.31	0.02	0.10	1.52	2.45	62	LSCS
Kashe	783	4.9	17	3.47	1S***			1.32	0.11	0.15	2.14	2.45	87	LSCS
Kirkness	2923	6.2	23	3.71	1S#		0.28		0.19		0.47	2.52	19	Ryan, pers. comm.
Eagle (Dryden Dist.)	27691	6.8	26	3.82	1S1W		0.68		0.75		1.73	2.56	67	Ryan, pers. comm.
Peninsula	865	9.0	35	3.89	1S***			1.29		0.19	1.48	2.58	57	LSCS
Doe	1187	5.9	25	4.24	4S***		1.00	0.67	0.98	0.57	3.37	2.68	126	LSCS
Lac Des Mille Lacs	2400	6.8	32	4.70	4S#		1.78		3.04		4.82	2.81	171	Ryan, pers. comm.
Redrock	363	6.2	30	4.83	19S***	0.41					0.41	2.85	14	Martin 1966
Stormer	303	3.3	22	6.67	1S#		1.05		2.22		3.27	3.29	99	Ryan, pers. comm.
Wendigo	419	9.2	64	6.96	1S#		0.96	1.61	1.07	0.02	3.66	3.35	109	Lacarte & Charles 1979
Davis	94	10.0	74	7.40	1S***			2.33		0.32	2.65	3.44	78	LSCS
Gullrock Complex	9628	6.9	52	7.54	1S		0.76		1.66		2.50	3.47	72	Ryan, pers. comm.
Esnagi	4362	5.9	46	7.80	1S#		1.80		1.54	0.02	3.44	3.53	97	Young 1972
Nipissing	85500	4.6	41	8.91	3Y		1.65		1.49	0.53	3.85	3.75	103	Anthony & Jorgensen 1977
Head	919	3.5	44	12.60	4S***			0.90		0.24	3.15	4.37	72	LSCS
Vaughn	3302	5.6	72	12.86	1S#		1.56		4.30		5.86	4.42	132	Ryan, pers. comm.
Cameron	1303	5.8	75	12.93	1S***			0.65	1.30	0.40	3.80	4.43	86	Lewis, pers. comm.
Balsam	4680	5.0	69	13.80	1S**			0.99	2.30	1.00	5.60	4.56	123	Lewis, pers. comm.
Coli	2125	2.5	35	14.00	1S#		0.63		1.18	0.04	1.85	4.62	40	Ryan, pers. comm.
Four Mile	742	8.5	134	15.76	4S***			0.90	0.41	0.03	1.91	4.84	39	LSCS
Gloucester Pool	1377	6.9	154	22.32	2Y		0.96	0.74	0.23	0.14	2.83	5.66	50	Campbell & Craig 1981a,d
Big Wolfe (Minn.)	425	8.5	202	23.76	5Y		5.26		4.83	4.26	15.12	5.82	260	Strand 1980
Onaman	11488	2.2	55	25.00	1S		0.16		0.92	0.01	1.10	5.96	18	Ryan, pers. comm.
Andrusia (Minn.)	611	7.9	202	25.57	5Y		3.02		3.25	2.69	9.52	6.02	158	Strand 1980
Cass (Minn.)	6313	7.6	202	26.58	5Y		1.01		2.02	2.80	6.16	6.13	100	Strand 1980

Table 1. (Continued)

Lake name	Area (ha)	Mean depth (m)	TDS ($mg\ell^{-1}$)	MEI	Length of record	Yields in kg $ha^{-1}yr^{-1}$							RYI% (100Y/Ŷ)	Sources of data
						Lake trout	N. pike	S.M. bass	Wall -eye	Yellow perch	Total (Y_t)	Poten -tial (Ŷ)		
St. John	618	4.3	116	26.98	3S##		0.72	0.05	0.42	0.28	2.18	6.17	35	Craig 1980; Campbell & Craig 1981b,e
Sparrow	1124	4.3	120	27.90	3S##		0.35	0.48	0.41	0.14	2.48	6.26	40	Craig 1980; Campbell & Craig 1981a,d
Severn Sound	13052	3.9	112	28.72	5S**		1.05	1.18	0.27	0.23	4.65	6.34	73	McNeil, pers. comm.
Sturgeon (Lindsay Dist).	4300	3.9	118	30.23	1S**			0.69	4.60	0.06	6.50	6.49	100	Lewis, pers. comm.
Lower Buckhorn	1234	3.5	115	32.86	1S***			0.78	3.49	0.01	5.04	6.74	75	LSCS
Pigeon	5342	3.2	109	34.06	1S***			1.52	2.40		4.58	6.85	67	Craig, pers. comm.
Whitefish	2850	2.0	74	37.00	1S##		1.83		3.71	3.43	8.97	7.11	126	Ryan, pers. comm.
Couchiching	4868	4.1	186	45.36	4S#		0.30	0.53	0.06	0.43	1.65	7.79	21	Campbell & Craig 1981a,c,e
Lovesick	257	2.5	116	46.40	1S***			1.89	5.80	0.71	8.61	7.87	109	LSCS
Rice Lake & Otonabie R.	10440	2.6	130	50.00	1S**			0.39	5.73	5.98	22.00	8.14	270	Lewis, pers. comm.
Dalrymple	1333	2.4	177	73.75	3S***		0.80	0.08	1.08		2.41	9.69	25	LSCS
Little	228	1.7	200	117.65	3S##		3.19	0.58	0.79	0.31	5.45	12.00	45	Craig 1980; Campbell & Craig 1981b,e
Orr	303	1.2	158	131.67	3S***		0.38	0.06		0.03	0.83	12.59	7	Craig 1980; Campbell & Craig 1981b,e
Scugog	6565	1.4	194	138.57	1S1W			0.02	2.10		3.10	12.88	24	Lewis, pers. comm.
Matchedash Bay	434	1.0	183	183.00	2S***		1.38	0.30	0.57	0.56	4.38	14.59	30	Campbell & Craig 1981b,e

*Summer fishing negligible
**Summer fishing only
***No winter fishing

#Winter fishing negligible
##Winter fishing but no records

S = Summer
W = Winter
Y = Seasons not distinguished in record
X = Species caught but yield negligible

Table 2. Ratios of species yield to total yield (Y_s/Y_t) and species yield to potential yield ($Y_s/\hat{Y}$) corresponding to the sport fisheries data given in Table 1, together with the overall mean, standard deviation, and sample size for each species.

Lake name	MEI	Yield in kg $ha^{-1}yr^{-1}$ Total Y_t	Yield in kg $ha^{-1}yr^{-1}$ Poten-tial $\hat{Y}$	Species yield/total yield (Y_s/Y_t) Lake trout	N. pike	S.M. bass	Wall-eye	Yellow perch	Species yield/potential yield ($Y_s/\hat{Y}$) Lake trout	N. pike	S.M. bass	Wall-eye	Yellow perch
Tahoe (Calif.)	0.20	0.27	0.67	1.00					0.40				
Chiblow-Denman	0.67	0.92	1.17	0.85		0.15			0.67		0.12		
Flack	0.79	1.24	1.26	1.00					0.98				
Kawagama	0.87	0.87	1.32	0.48		0.25		0.25	0.32		0.17		0.17
Joseph	0.99	0.84	1.39	0.39		0.18			0.24		0.11		
Redstone	1.00	1.54	1.40	0.90				0.0065	0.99				0.0096
Lake of Bays (Bracebridge Dist.)	1.03	0.21	1.42	0.19		0.43		0.14	0.028		0.063		0.021
Rosseau	1.14	0.45	1.48	0.11		0.044		0.15	0.034		0.013		0.047
Little Quirke	1.26	0.33	1.55	1.00					0.21				
Semiwite	1.31	0.76	1.58	1.00					0.48				
Clearwater (Minn.)	1.37	0.25	1.61	1.00					0.15				
Darragh	1.43	0.82	1.64	1.00					0.50				
Bone	1.53	1.97	1.69	1.00					1.16				
Opeongo	1.57	0.33	1.72	1.00					0.19				
Happy Isle	1.77	0.28	1.81	1.00					0.15				
Mississagua	1.92	0.93	1.88	0.32		0.54		0.04	0.16		0.27		0.021
Haliburton	2.01	0.62	1.92	0.48		0.43			0.16		0.14		
Bernard	2.02	1.23	1.92	0.37		0.34		0.16	0.23		0.22		0.10
Temagami	2.03	0.46	1.93	0.63		0.04	0.19		0.15		0.010	0.047	
Jimchrist	2.16	1.62	1.98	1.00					0.82				
Lavieille	2.29	0.57	2.03	0.68					0.19				
Drag	2.33	0.68	2.05	0.30		0.54		0.06	0.10		0.18		0.019
Pevensey	2.42	1.67	2.08	0.38				0.62	0.30				0.49
Gull	2.48	1.96	2.11	0.91		0.02		0.02	0.84		0.014		0.014
Mountain	2.69	1.74	2.18			0.41					0.32		
Pickerel	2.79	2.59	2.22		0.51	0.09	0.39	0.01		0.60	0.11	0.45	0.0090
Sturgeon (Ignace Dist.)	2.79	0.42	2.22	0.71	0.19		0.10		0.13	0.036		0.018	
Merchant	3.03	0.66	2.30	1.00					0.29				

Table 2. (Continued)

Lake name	MEI	Yield in kg ha^{-1}yr^{-1}		Species yield/total yield (Y_s/Y_t)					Species yield/potential yield ($Y_s/\hat{Y}$)				
		Total Y_t	Potential $\hat{Y}$	Lake trout	N. pike	S.M. bass	Wall-eye	Yellow perch	Lake trout	N. pike	S.M. bass	Wall-eye	Yellow perch
Red 2 & 4	3.04	1.46	2.31		0.37		0.63			0.23		0.40	
Spring	3.15	0.60	2.35	1.00					0.25				
Red 1	3.21	1.08	2.37	0.19	0.55		0.26		0.089	0.25		0.12	
Northern Light	3.21	0.55	2.37	0.13	0.04	0.09	0.45		0.029	0.0084	0.021	0.10	
Eagle (Bracebridge Dist.)	3.44	1.41	2.44		0.02	0.65	0.01	0.31		0.012	0.38	0.0041	0.18
Kashagawigamog	3.46	1.52	2.45	0.07		0.20	0.01	0.07	0.045		0.13	0.0082	0.040
Kashe	3.47	2.14	2.45			0.62	0.05	0.07			0.54	0.045	0.061
Kirkness	3.71	0.47	2.52		0.59		0.40			0.11		0.075	
Eagle (Dryden Dist.)	3.82	1.73	2.56		0.36		0.43			0.25		0.29	
Peninsula	3.89	1.48	2.58			0.87		0.13			0.58		0.074
Doe	4.24	3.37	2.68		0.30	0.20	0.30	0.17		0.37	0.25	0.36	0.21
Lac Des Mille Lacs	4.70	4.82	2.81		0.37		0.63			0.63		1.08	
Redrock	4.83	0.41	2.85	1.00					0.14				
Stormer	6.67	3.27	3.29		0.32		0.68			0.32		0.67	
Wendigo	6.96	3.66	3.35		0.26	0.44	0.29	0.01		0.29	0.48	0.32	0.0060
Davis	7.40	2.65	3.44			0.88		0.12			0.68		0.093
Gullrock Complex	7.54	2.50	3.47		0.30		0.66			0.22		0.48	
Esnagi	7.80	3.44	3.53		0.52		0.45			0.51		0.44	
Nipissing	8.91	3.85	3.75		0.43		0.39	0.14		0.44		0.40	0.14
Head (Laxton Twp.)	12.60	3.15	4.37			0.28		0.08			0.20		0.055
Vaughn	12.86	5.86	4.42		0.27		0.73			0.35		0.97	
Cameron	12.93	3.80	4.43			0.17	0.34	0.10			0.15	0.29	0.090
Balsam	13.80	5.60	4.56			0.18	0.41	0.18			0.22	0.50	0.22
Coli	14.00	1.85	4.62		0.34		0.64	0.02		0.14		0.25	0.0087
Four Mile	15.76	1.91	4.84			0.47	0.21	0.01			0.19	0.085	0.0062
Gloucester Pool	22.32	2.83	5.66		0.34	0.26	0.08	0.05		0.17	0.13	0.041	0.025
Big Wolfe (Minn.)	23.76	15.12	5.82		0.35		0.32	0.28		0.90		0.83	0.73
Onaman	25.00	1.10	5.96		0.15		0.84	0.01		0.027		0.15	0.0017
Andrusia (Minn.)	25.57	8.50	6.02		0.32		0.34	0.28		0.50		0.54	0.45
Cass (Minn.)	26.58	5.50	6.13		0.16		0.33	0.45		0.16		0.33	0.46

Table 2. (Continued)

Lake name	MEI	Yield in kg $ha^{-1}yr^{-1}$ Total Y_t	Yield in kg $ha^{-1}yr^{-1}$ Potential $\hat{Y}$	Species yield/total yield (Y_s/Y_t) Lake trout	N. pike	S.M. bass	Wall-eye	Yellow perch	Species yield/potential yield ($Y_s/\hat{Y}$) Lake trout	N. pike	S.M. bass	Wall-eye	Yellow perch
St. John	26.98	2.18	6.17		0.33	0.02	0.19	0.13		0.12	0.0081	0.068	0.045
Sparrow	27.90	2.48	6.26		0.14	0.19	0.17	0.06		0.056	0.077	0.065	0.022
Severn Sound	28.72	4.65	6.34		0.22	0.25	0.06	0.05		0.16	0.19	0.043	0.037
Sturgeon (Lindsay Dist.)	30.23	6.50	6.49			0.11	0.71	0.0092			0.11	0.71	0.0092
Lower Buckhorn	32.86	5.04	6.74			0.15	0.69	0.01			0.11	0.52	0.0015
Pigeon	34.06	4.58	6.85			0.33	0.52				0.22	0.35	
Whitefish	37.00	8.97	7.11		0.20		0.41	0.38		0.26		0.52	0.48
Couchiching	45.36	1.65	7.79		0.18	0.32	0.04	0.26		0.038	0.068	0.0077	0.055
Lovesick	46.40	8.61	7.87			0.22	0.67	0.08			0.24	0.74	0.0090
Rice Lake & Otonabie River	50.00	22.00	8.14			0.02	0.26	0.27			0.048	0.70	0.73
Dalrymple	73.75	2.41	9.69		0.33	0.03	0.45			0.083	0.0083	0.11	
Little	117.65	5.45	12.00		0.59	0.11	0.15	0.06		0.26	0.048	0.066	0.026
Orr	131.67	0.83	12.59		0.46	0.07		0.04		0.030	0.0048		0.0024
Scugog	138.57	3.10	12.88			0.01	0.68				0.0016	0.16	
Matchedash Bay	183.00	4.38	14.59		0.31	0.07	0.13	0.13		0.095	0.021	0.039	0.038
Number of lakes in sample				31	31	40	42	40	31	31	40	42	40
Mean Y_S/Y_t and $Y_S/\hat{Y}$				0.680	0.317	0.267	0.374	0.135	0.330	0.246	0.171	0.319	0.130
Standard Deviation				0.345	0.146	0.226	0.231	0.136	0.304	0.212	0.165	0.286	0.196

Table 3. Morphometric, total dissolved solids (TDS), length of fishing records and yield data for the commercial fisheries used here as a basis for partitioning the potential yield ($\hat{Y}$) by species, where $\hat{Y} = 1.4(MEI)^{0.45}$.

Lake name	Area (ha)	Mean depth (m)	TDS ($mg\ell^{-1}$)	MEI	Years of record	Yields in $kg\ ha^{-1}yr^{-1}$						RYI% ($100Y/\hat{Y}$)	Source of data
						Lake trout	White -fish	N. pike	Wall -eye	Total (Y_t)	Poten -tial ($\hat{Y}$)		
Lawrence	1871	22.2	28	1.27	14	0.19	0.28		0.45	1.40	1.56	90	Adams & Olver 1977
Nipigon	448060	54.9	80	1.46	57	0.13	0.63	0.01	0.11	0.95	1.60	59	Adams & Olver 1977
Red	17676	14.6	32	2.19	42	0.03	0.68	0.07	0.21	1.24	1.99	62	Adams & Olver 1977
Atikwa	5388	13.2	29	2.20	15	0.15	0.65	0.11	0.54	1.65	1.99	83	Adams & Olver 1977
Lake of Bays (Ignace Dist.)	4662	12.2	35	2.84	43	0.09	0.24	0.33	0.45	1.18	2.24	53	Adams & Olver 1977
Eagle (Dryden Dist.)	27691	6.8	26	3.82	40	0.03	0.69	0.30	0.41	2.08	2.56	81	Adams & Olver 1977
Marchington	3640	8.0	31	3.87	12		0.33	0.30	0.50	1.56	2.57	60	Adams & Olver 1977
Nungessier	7557	5.2	21	4.04	13		0.27	0.15	0.83	1.43	2.62	54	Adams & Olver 1977
Penassi	1441	6.6	27	4.11	15	0.05	0.28	0.29	0.56	1.27	2.64	48	Adams & Olver 1977
Basket	4267	6.0	26	4.33	35	0.01	0.71	0.42	0.66	2.21	2.71	82	Adams & Olver 1977
Hooker	2113	5.8	31	5.34	11	0.01	1.14	0.06	0.85	2.08	2.98	70	Adams & Olver 1977
Gullrock	6762	7.8	44	5.64	26	0.01	0.76	0.14	0.63	1.88	3.05	62	Adams & Olver 1977
Wintering	1688	5.3	31	5.78	28		0.12	0.71	0.78	2.07	3.08	67	Adams & Olver 1977
Confusion	1426	11.4	76	6.66	10	0.11	0.75	0.10	0.60	1.83	3.20	57	Adams & Olver 1977
MacDowell	10360	6.1	41	6.72	24		1.02	0.26	1.08	2.60	3.30	79	Adams & Olver 1977
Cliff	2263	10.6	74	6.98	13	0.13	1.27	0.16	0.09	1.68	3.36	51	Adams & Olver 1977
Little Trout	3665	6.7	47	7.01	17		1.34	0.25	0.44	2.09	3.36	62	Adams & Olver 1977
Lake of the Woods	246760	7.2	83	9.58	50		0.34	0.68	1.14	3.15	3.87	82	Adams & Olver 1977
Raggedwood	1118	6.6	64	9.70	11	0.04	0.99	0.05	0.76	1.89	3.89	48	Adams & Olver 1977
Weagamow (Round)	12430	6.7	67	10.00	22		1.40	0.03	0.55	1.98	3.90	51	Adams & Olver 1977
Clay	3088	7.9	90	11.39	32		0.52	0.50	0.67	2.80	4.18	67	Adams & Olver 1977
Windigo	8550	7.3	84	11.51	16	*	1.95	0.06	0.25	2.27	4.20	55	Adams & Olver 1977
Superior	8.24×10^6	148.4	60	0.40	43	0.24				0.98	0.93	105	Baldwin & Saalfeld 1962
Michigan	5.80×10^6	84.1	118	1.40	35	0.49	0.15			1.80	1.63	110	Baldwin & Saalfeld 1962
Reindeer	89580	17.9	26	1.45	18	0.79	1.45		0.10	2.34	1.66	141	Schlick (pers. comm.)
Cree	115562	14.9	22	1.48	11	0.97	0.04	<0.01	<0.01	1.04	1.67	62	Rawson 1959
Ontario	1.95×10^6	80.5	155	1.93	28	0.12	0.29			1.07	1.88	57	Baldwin & Saalfeld 1962
Huron	5.96×10^6	59.4	117	1.97	52	0.43	0.24			1.45	1.90	76	Baldwin & Saalfeld 1962
Wollaston	206251	17.4	35	2.01	12	0.65	0.49	<0.01	0.01	1.18	1.92	61	Rawson 1959
Athabasca	789964	25.9	58	2.24	19	0.29	0.10			0.42	2.01	21	Rawson 1947
LaRonge	142542	12.5	130	10.40	28	0.36	0.37	0.04	0.07	0.93	4.02	23	Rawson & Atton 1953

*Species present but yield data not reliable because of quotas or other factors.

Table 4. Ratios of species yield to total yield (Y_s/Y_t) and species yield to potential yield ($Y_s/\hat{Y}$) corresponding to the commercial fisheries data given in Table 3, together with the overall mean, standard deviation and sample size for each species.

Lake name	MEI	Yields in kg ha^{-1}yr^{-1}		Species yield/total yield (Y_s/Y_t)				Species yield/ potential yield ($Y_s/\hat{Y}$)			
		Total Y_s	Poten-tial $\hat{Y}$	Lake trout	White-fish	North. pike	Wall-eye	Lake trout	White-fish	North. pike	Wall-eye
Lawrence	1.27	1.40	1.56	0.14	0.20		0.32	0.12	0.18		0.29
Nipigon	1.46	0.95	1.60	0.14	0.66	0.010	0.11	0.081	0.39	0.0063	0.069
Red	2.19	1.24	1.99	0.024	0.55	0.056	0.17	0.015	0.34	0.035	0.10
Atikwa	2.20	1.65	1.99	0.091	0.39	0.067	0.33	0.075	0.33	0.055	0.27
Lake of Bays (Ignace Dist.)	2.84	1.18	2.24	0.076	0.20	0.28	0.38	0.040	0.11	0.15	0.20
Eagle (Dryden Dist.)	3.82	2.08	2.56	0.014	0.33	0.14	0.20	0.012	0.27	0.12	0.16
Marchington	3.87	1.56	2.57		0.21	0.19	0.32		0.13	0.12	0.19
Nungesser	4.04	1.43	2.62		0.19	0.10	0.58		0.10	0.057	0.32
Penassi	4.11	1.27	2.64	0.039	0.22	0.23	0.44	0.019	0.11	0.11	0.21
Basket	4.33	2.21	2.71	0.0045	0.32	0.19	0.30	0.0037	0.26	0.15	0.24
Hooker	5.34	2.08	2.98	0.0048	0.55	0.029	0.41	0.0034	0.38	0.020	0.28
Gullrock	5.64	1.88	3.05	0.0053	0.40	0.074	0.33	0.0033	0.25	0.046	0.21
Wintering	5.78	2.07	3.08		0.058	0.34	0.38		0.039	0.23	0.25
Confusion	6.66	1.83	3.20	0.060	0.41	0.055	0.33	0.034	0.23	0.031	0.19
MacDowell	6.72	2.60	3.30		0.39	0.10	0.41		0.31	0.079	0.33
Cliff	6.98	1.68	3.36	0.077	0.76	0.095	0.054	0.039	0.38	0.048	0.027
Little Trout	7.01	2.09	3.36		0.64	0.12	0.21		0.40	0.074	0.13
Lake of the Woods	9.58	3.15	3.87		0.11	0.21	0.36		0.088	0.17	0.29
Raggedwood	9.70	1.89	3.89	0.021	0.52	0.026	0.40	0.010	0.25	0.013	0.19
Weagamow (Round)	10.00	1.98	3.90		0.71	0.016	0.28		0.36	0.0077	0.14
Clay	11.39	2.80	4.18		0.18	0.18	0.24		0.12	0.12	0.16
Windigo	11.51	2.27	4.20	*	0.86	0.026	0.11		0.46	0.014	0.059
Number of lakes in sample					↓	21	22		↓	21	22
Mean Y_s/Y_t & $Y_s/\hat{Y}$						0.121	0.303			0.0789	0.196
Standard Deviation						0.0904	0.124			0.0620	0.0850

Table 4. (Continued)

Lake name	MEI	Yields in kg $ha^{-1}yr^{-1}$		Species yield/total yield (Y_s/Y_t)				Species yield/potential yield ($Y_s/\hat{Y}$)			
		Total Y_s	Poten-tial $\hat{Y}$	Lake trout	White-fish	North. pike	Wall-eye	Lake trout	White-fish	North. pike	Wall-eye
Superior	0.40	0.98	0.93	0.24				0.26			
Michigan	1.40	1.80	1.63	0.27	0.08			0.30	0.09		
Reindeer	1.45	2.34	1.66	0.34	0.62		0.04	0.48	0.87		0.06
Cree	1.48	1.04	1.67	0.93	0.04	0.00	0.00	0.58	0.02	0.00	0.00
Ontario	1.93	1.07	1.88	0.11	0.28			0.06	0.15		
Huron	1.97	1.45	1.90	0.30	0.17			0.23	0.13		
Wollaston	2.01	1.18	1.92	0.55	0.42	0.00	0.01	0.34	0.26	0.00	0.01
Athabasca	2.24	0.42	2.01	0.69	0.24			0.14	0.05		
LaRonge	10.40	0.93	4.02	0.39	0.40	0.04	0.08	0.09	0.09	0.01	0.02
Number of lakes in sample				9	30			9	30		
Mean Y_s/Y_t & $Y_s/\hat{Y}$				0.424	0.370	*	*	0.280	0.238	*	*
Standard Deviation				0.256	0.221			0.170	0.173		

*Not a target species here.

RESULTS

Community structure or species composition

The sport fisheries lakes in Table 1 are arranged in ascending order of MEI, while the fish species are in taxonomic order. A glance at the table shows a change in species composition with increase in MEI similar to that suggested by Colby *et al.* (1972) in the SCOL Symposium. The lake trout lakes had MEIs ranging from 0.2 to 4.83 whereas the northern pike and walleye lakes had MEIs of 2.79 to 183.0. Smallmouth bass were found in lakes having MEI values ranging from 0.67 to 183.0 but their absence from some of the more northern lakes with low MEI values was probably due to unsuitable temperature conditions (Fry and Watt 1955; Shuter *et al.* 1980).

The commercial fisheries lakes were also arranged in ascending order of MEI and the fish species in taxonomic order in Table 3. The MEI for the lake trout lakes ranged from 0.4 to 2.2, except for la Ronge where it was 10.4. For the whitefish, pike, walleye lakes, the MEIs were 1.5 to 11.5. Thus, there was more overlap seen in MEI values for lake trout and percid lakes fished commercially than in the sport fisheries data set, but the range of MEI values was narrower.

Relations between species, total and potential yields

Lake trout - Angling yields for this species averaged 68% of the total angling yield of all species and 33% of the potential yield estimated from the MEI formula, whereas the commercial yield of lake trout averaged 42% of the total yield and 28% of the potential yield. The differences between the sport and commercial percentages are due, in part, to the high degree of selectivity for lake trout by anglers and also to the disproportionate weights of the various species in the total catch. An average size lake trout tends to be

much heavier than an average size smallmouth bass, for example, and therefore makes up a larger part of the total weight of fish caught. Hence, the above ratios for lake trout sport fisheries are probably somewhat inflated. The alternative procedure of using the Lake Opeongo trout fishery as a model (Fig. 3) indicates that the allowable yield for lake trout should be 16% of the potential yield. The latter value is probably too stringent, particularly where there is a demand for winter sport fisheries: a value half way between the 16% and 33% estimates, say 25%, would appear to be reasonable compromise. Therefore, our recommended allowable yield for both sport and commercial lake trout fisheries is 25% of the potential yield estimated from the MEI.

Brook trout - Most of the available data for brook trout yields are from lakes having artificially maintained stocks and, therefore, are not considered in this report. In Redrock Lake and Lake Lavieille in Algonquin Park, Ontario, which have self-sustaining brook trout populations, yields of this species have averaged 0.41 kg. ha^{-1} or 14% of the potential yield and 0.18 kg ha^{-1} or 9% of the potential yield, respectively. For Moosehead Lake in Maine, which has a self-sustaining community of brook trout, lake trout and landlocked salmon, the brook trout yields have apparently averaged about 0.04 kg ha^{-1} yr^{-1} or about 9% of the potential yield (AuClair 1978). These yields are comparable to those of lake trout lakes in Ontario (Martin and Olver 1980) and, as in the case of the lake trout, self-sustaining brook trout populations most commonly occur in "low yield situations" (Fraser 1963) characterized by MEI values less than 5.0.

In Saddle Lake, a single species fishery in the Sault Ste. Marie District, the yield of brook trout in 1968 (winter and summer) was 2.05 kg ha^{-1} or 56% of the potential yield (M.-F. Bernier,pers. comm.). Yield for the winter fishery only, over a 3 year period (1968-70) averaged 0.87 kg ha^{-1} or 24% of the potential yield, but there was a progressive decline in the catch

each winter from 39% of the potential yield in 1968 to 24% in 1969 and 8.0% in 1970. The C.U.E.s for the winters of 1969 (0.067 fish per angler-hr) and 1970 (0.061) were much less than that for the winter of 1968 (0.189). These observations suggest that the catch in 1968 was excessive.

We feel that, with the exception of the Saddle Lake data, these brook trout yields are low. Therefore, we suggest that until additional data are obtained that the guidelines recommended for lake trout (25% of the potential yield) be applied to naturally reproducing populations of brook trout also.

Lake whitefish - Although this species may be an important component of sport fish catches in certain lakes, such as Simcoe and Temagami, they contributed less than 0.10 kg ha^{-1} yr^{-1} to total catches in lakes from our sample. In some instances they are caught incidental to lake trout angling. P. Waring (pers. comm.) estimates that lake whitefish yields from Lake Simcoe during the years 1965, 66 and 68, before that fishery collapsed, were from 2.1 to 2.5 kg ha^{-1} yr^{-1} . Almost all of this was taken by winter angling. It amounts to 65-75% of the average annual yield for all species or 50-60% of the potential yield (4.23 kg ha^{-1} yr^{-1}) for Lake Simcoe. Although this appears high, whitefish population estimates indicate that overexploitation was not a contributing factor to the collapse of the whitefish population in the early 1970s (DesJardine and Lawrence 1977).

For our sample of commercial fisheries the whitefish yields averaged 37% of the total yield and 24% of the potential yield. We suggest, therefore, that the latter figure be taken as the allowable yield of whitefish for commercial fisheries. Although our data are limited, the same guideline does not appear to be unreasonable for sport fisheries.

Northern pike - There is a marked difference between the importance of this species in the commercial and sport fisheries. In the commercial

fisheries the yield of this species averaged 12% of the total catch and 8% of the potential yield, whereas in the sport fisheries it comprised 32% of the total catch and 25% of the potential yield. The low values for the commercial fisheries are probably underestimated owing to fluctuations in market demand for this species and underexploitation. The higher values for the sport fisheries suggest that northern pike is a target species in some instances, particularly for tourists on the northern lakes. Our recommended value for northern pike is 25% for sport fisheries and 10-20% for the commercial fishery.

Smallmouth bass - Angling yields of this species averaged 27% of the total angling yield and 17% of the potential yield for the smallmouth bass fisheries in our sample. However, 17% of the potential yield may be an underestimate of the allowable yield in some instances, since the smallmouth bass was caught incidental to fishing for lake trout, northern pike or walleye in many of these lakes. Furthermore, some of the lakes in our sample are outside the climatic range for optimum production of smallmouth bass (Shuter *et al.* 1980). In lakes where smallmouth bass is the prime target species and climatic conditions are optimal the allowable yield can probably be much higher than 17% of the potential yield, say 50%.

Walleye - Commercial yields of walleye averaged 30% of the total commercial yield and 20% of the potential yield. These are essentially the same values obtained earlier by Adams and Olver (1977). The angling yield for walleye averaged 37% of the total sport fish yield and 32% of the potential yield. Therefore, the guideline values for walleye are 20% of the potential yield for commercial fisheries and 32% for sport fisheries.

We feel that these values are satisfactory for the commercial fisheries, which tend to select for large, mature fish. However, they may be too low for sport fisheries, which tend to select the smaller, immature fish and

may allow a significant proportion of potential spawners to escape.

Yellow perch - The yield of perch from the sport fisheries cited in Tables 1 and 2 averaged 14% of the total angling yield and 13% of the potential yield. In many cases yellow perch are caught incidental to other species and the fishery tends to be seasonal. Even though large numbers of perch may be caught, their small individual size relative to other species makes their contribution to the total weight caught usually very small. For example, yellow perch yields from Lake Simcoe for 1965, 66 and 68 only averaged about 0.15 kg ha^{-1} or 4% of the total catch (P. Waring, pers. comm.), even though the spring perch run at Atherley Narrows is an important event on the angling calendar. Based on these observations the recommended guideline value for yellow perch sport fisheries is in the order of 13% of the potential yield.

The yellow perch was not an important component of the commercial fish harvest in our set of lakes. A notable exception is Lake Erie where this species has been intensively exploited. Data derived from Hartman *et al.* (1980) show that during the 1960s the annual commercial yield of yellow perch averaged 3.88 kg ha^{-1} or 94% of the potential yield and these authors state that "these stocks have shown clear, classic signs of distress and deterioration since at least 1969". Because we have so little information on commercial harvests of yellow perch from Ontario waters, we cannot recommend an allowable commercial yield for this species at present.

Guidelines

On the basis of the foregoing information, and subject to the qualifications stated later, the following guidelines are recommended for partitioning the potential fish production estimated from Ryder's MEI formula into individual species yields:

Species	Recommended % of $\hat{Y} = 1.4(MEI)^{0.45}$	
	Sport fisheries	Commercial fisheries
Brook trout	25	N/A
Lake trout	25	25
Lake whitefish	24	24
Northern pike	25	10-20
Smallmouth bass	17-50	N/A
Walleye	32	20
Yellow perch	13	?

Here N/A indicates that the guidelines are not applicable.

Where there is both a sport and commercial fishery for the same species, the values for the two types of fishery should not be added together. Rather, the total yield for the sport and commercial fishery combined should not exceed the larger of the two figures given for the species. For example, the combined yield for a commercial and sport fishery for walleye should not exceed 32% of the potential yield.

In view of the concern of Larkin and others, cited above, we feel that with the possible exception of certain walleye sport fisheries, the total yield of all species in commercial, sport or combined commercial and sport fisheries should be less than 100% of the potential yield, to provide a margin of safety in managing the fishery. Since there are few bodies of water in Ontario where the catch is comprised of more than 2 or 3 target species, this is not likely to be a problem, provided the above guidelines for catches of individual species are adhered to. For example, the recommended catch for a whitefish, pike, walleye commercial fishery would be 54% to 64% of the potential yield.

For a pike, smallmouth bass, walleye sport fishery, the total catch would be in the order of 74%+, depending on how intensively the bass were harvested.

Should the species yields for some multi-species fisheries sum to more than 100% of the potential yield estimated from the MEI, we suggest that the guideline yields recommended here be scaled down so that the sum of species yields does not exceed the potential yield; especially if there is evidence in the demographic characteristics of the catches that a species is threatened with overexploitation.

DISCUSSION

Procedure for applying the guidelines

The nomogram in Fig. 4 shows the relationship between MEI, potential fish yields, and species yields at various levels of exploitation, where the latter equals species yield/potential yield expressed as a percentage. The data from which this nomogram was prepared are shown in Table 5. For example, if a lake has an MEI of 4.5 (top scale), the corresponding potential yield is 2.75 (bottom scale). The next step is to select the appropriate curve for the desired or recommended level of exploitation (right hand scale). Then find the intersection of this curve with the vertical line dropped from the MEI and project this point onto the left hand scale to find the species yield. In the present case, if we choose an exploitation level of 25%, the yield for the species in question would be 0.69 kg ha^{-1} yr^{-1}.

If we follow this procedure for lake trout in a lake with an MEI of 3.0, the potential yield for all species would be 2.30 kg ha^{-1} yr^{-1}. For a 25% level of exploitation, the lake trout yield would be 0.58 kg ha^{-1} yr^{-1} which is within the 0.25 and 0.75 kg ha^{-1} yr^{-1} range suggested by Martin and Olver (1980) for viable lake trout fisheries. On the other hand, if we had selected an exploitation level of 50%, the yield of lake trout would have been 1.15 kg ha^{-1} yr^{-1} and thus a cause for some concern.

For a multispecies fishery, select the exploitation level for each individual species on the right hand scale and, using the above procedure, find the yield for each species on the left hand scale. These are then summed to get the total allowable yield.

The following example shows the relationship between the recommended level of exploitation, the corresponding species yield and the actual yields for the commercial fishery for lake whitefish, northern pike, and walleye from

Figure 4. Nomogram relating MEI, potential fish production ($\hat{Y}$) and species yield (Y_s) at various levels of exploitation, where the latter equals species yield/potential yield expressed as a percentage ($= 100Y_s/\hat{Y}$).

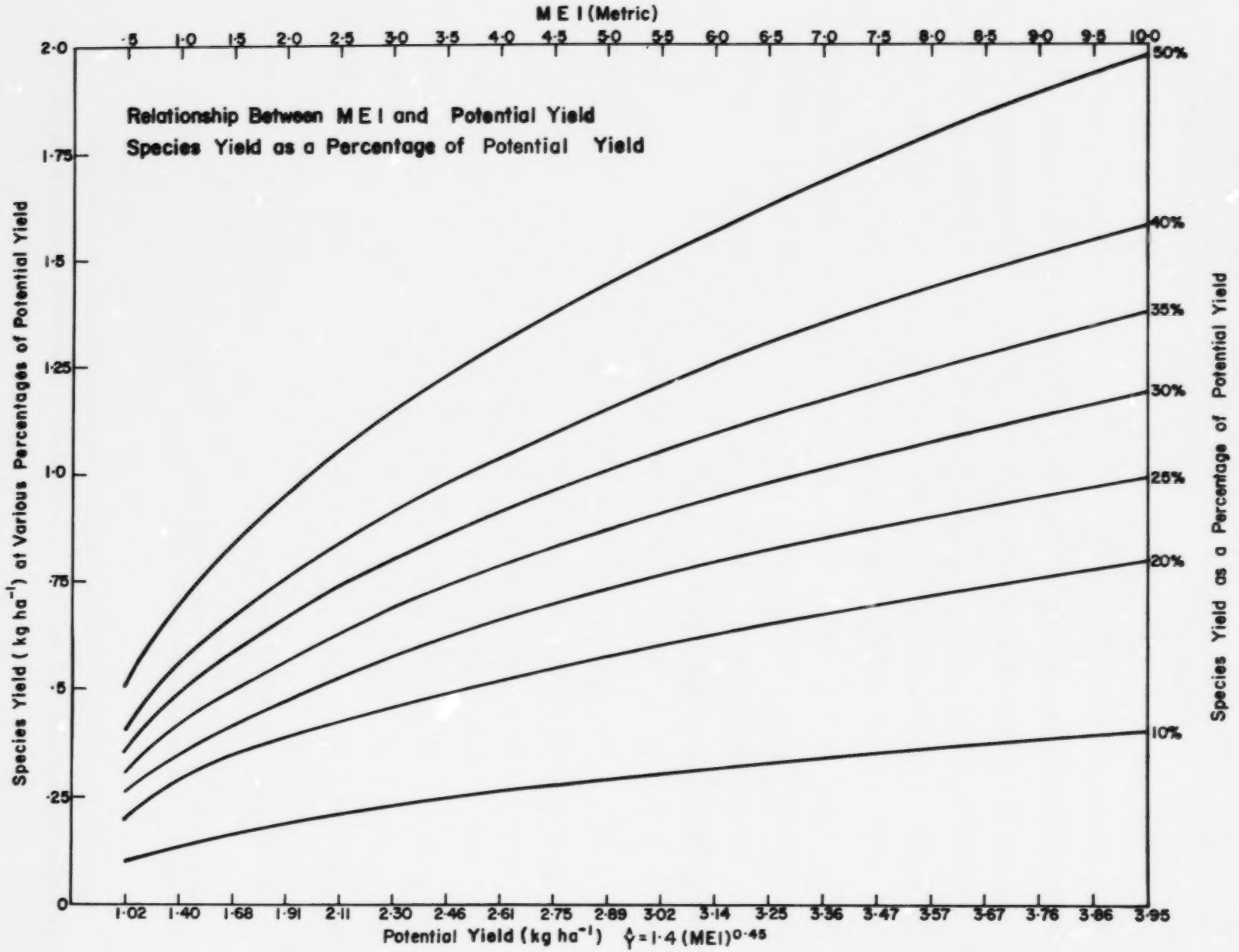

MEI (Metric)
·5 1·0 1·5 2·0 2·5 3·0 3·5 4·0 4·5 5·0 5·5 6·0 6·5 7·0 7·5 8·0 8·5 9·0 9·5 10·0
Relationship Between MEI and Potential Yield
Species Yield as a Percentage of Potential Yield
Species Yield (kg ha⁻¹) at Various Percentages of Potential Yield
2·0
1·75
1·5
1·25
1·0
·75
·5
·25
0
50%
40%
35%
30%
25%
20%
10%
Species Yield as a Percentage of Potential Yield
1·02 1·40 1·68 1·91 2·11 2·30 2·46 2·61 2·75 2·89 3·02 3·14 3·25 3·36 3·47 3·57 3·67 3·76 3·86 3·95
Potential Yield (kg ha⁻¹) $\hat{Y} = 1{\cdot}4\,(MEI)^{0{\cdot}45}$

Table 5. Relationship between MEI, potential fish production and species yield at various levels of exploitation. These data were used in plotting the nomogram in Fig. 4.

MEI (metric)	Potential fish production[1] (kg ha^{-1})	Species yields at various levels of exploitation (%)						
		10	20	25	30	35	40	50
0.5	1.02	.10	.20	.26	.31	.36	.41	.51
1.0	1.40	.14	.28	.35	.42	.49	.56	.70
1.5	1.68	.17	.34	.42	.50	.59	.67	.84
2.0	1.91	.19	.38	.48	.57	.67	.76	.96
2.5	2.11	.21	.42	.53	.63	.74	.84	1.06
3.0	2.30	.23	.46	.58	.69	.81	.92	1.15
3.5	2.46	.25	.49	.62	.74	.86	.98	1.23
4.0	2.61	.26	.52	.65	.78	.91	1.04	1.31
4.5	2.75	.28	.55	.69	.83	.96	1.10	1.38
5.0	2.89	.29	.58	.72	.87	1.01	1.16	1.45
5.5	3.02	.30	.60	.76	.91	1.06	1.21	1.51
6.0	3.14	.31	.63	.79	.94	1.10	1.26	1.57
6.5	3.25	.32	.65	.81	.98	1.14	1.30	1.63
7.0	3.36	.34	.67	.84	1.01	1.18	1.34	1.68
7.5	3.47	.35	.69	.87	1.04	1.21	1.39	1.74
8.0	3.57	.36	.71	.89	1.07	1.25	1.43	1.79
8.5	3.67	.37	.73	.92	1.10	1.28	1.47	1.84
9.0	3.76	.38	.75	.94	1.13	1.32	1.50	1.88
9.5	3.86	.39	.77	.97	1.16	1.35	1.54	1.93
10.0	3.95	.40	.79	.99	1.19	1.38	1.58	1.98

[1]Derived from formula $\hat{Y} = 1.4(MEI)^{0.45}$

MacDowell Lake (Table 3), which has an MEI of about 9 and a potential yield of 3.76 kg. ha^{-1} yr^{-1}.

Species	Recommended exploitation level (%)	Allowable species yield kg ha^{-1} yr^{-1}	Actual species yield kg ha^{-1} yr^{-1}
Lake whitefish	24	0.90	1.02
Northern pike	10	0.38	0.26
Walleye	20	0.75	1.08

When one compares the allowable species yields with the actual species yields, it appears that the northern pike in this lake are not being overexploited but that the walleye, and possibly the whitefish, may be to some extent.

Qualification of the guidelines

It should be emphasized that the MEI formula and the guidelines given here apply only to game and commercial fish species in self-sustaining populations. They also apply only to lakes and not to streams and rivers. Lakes with two or more distinct basins may pose special problems owing to marked differences in MEI, species or stocks of fish present, age class structures and intensity of exploitation. In some instances, it may be advisable to treat each basin as an individual lake (Schupp 1978; Hough, Stansbury and Michalski 1980). However, this solution may not be entirely satisfactory, since the fish may separate by age groups or migrate from one basin to another with the passage of the seasons.

A "rule of thumb" sometimes used by FAO fisheries scientists (H. Regier, pers. comm.) states that the 95% confidence limits on an estimate of potential yield (or MSY_c) based on the MEI solely vary by a factor of about 3. That is,

the actual value may be from 1/3 to 3 times the estimated value and the upper bound to the confidence interval is 9 times the lower. Hence fisheries managers should realize that present yield estimates will probably have to be revised as more information and more complete mathematical models become available. The following are some features which may have to be taken into account when adjusting the guidelines in the meantime.

Heavily exploited fisheries - Where there is additional evidence to indicate that the fishery may be in trouble, e.g., a scarcity of mature fish in the fisherman's catches or in catches from experimental netting, the lower guideline value or values less than the guideline recommendation should be used. Present day poor catches may be the result of overexploitation in the past. For other criteria, which may be used in detecting overexploitation, refer to the guidelines provided by SPOF Working Group 15.

Destruction of habitat - Where the fish are subjected to additional stresses, such as water pollution or loss of spawning grounds and other habitat, the guidelines given here for allowable species yields should be reduced to some extent, at the fisheries manager's discretion. An indication of how a disturbance of the littoral zone may affect fish yields can be seen on comparing the data for Orr and Little Lakes at the bottom of Table 1. These two lakes have the same MEIs and, hence, the same potential yields. However, the anglers take 45% of the potential yield from Little Lake but only 7% from Orr Lake. Most of the shoreline of Little Lake is marsh and undeveloped, whereas about 80-90% of the shoreline of Orr Lake is taken up by cottages (R. Craig, pers. comm.). That the effects of habitat alteration on fish production can be very subtle has been demonstrated by Bidgood (1973).

Energy input and applicability of the MEI formula - The form of the MEI equation given in this report ($\hat{Y} = 1.4(MEI)^{0.45}$) is applicable to north-temperate lakes which are considered to have similar solar energy input. However, there can be substantial differences in energy input from north to

south in the temperate zone, which cause increased variance in the model. The manager must be cognizant of where his or her lake is located in this range and whether the actual value of the potential yield is likely to be higher or lower than that estimated from the above formula.

Energy utilization and compensatory mechanisms - It may be that the potential yields for some percid fisheries are underestimated by the MEI formula. Walleye and perch fisheries are often concentrated in relatively shallow lakes or bays where turnover and recycling of solar energy and materials is highly efficient. In contrast, oligotrophic lakes tend to be energy and nutrient sinks. In lakes where there is a highly efficient turnover of energy, compensatory mechanisms in the fish stocks (such as increased growth rate, earlier maturity and greater fecundity) may operate at a higher level than in lakes which are nutrient sinks. Compensatory mechanisms are also likely to be more effective in southern waters with high energy input than in northern waters.

Method of capture and compensatory mechanisms - There is increasing evidence that the method or gear used in catching the fish may affect the potential yield for a species or a community of fish. For example, if anglers catch younger fish than commercial fishermen, and still allow sufficient mature fish to escape to ensure reproduction, case histories and bioenergetic principles suggest that more weight could be taken safely by anglers than by commercial fishermen. Because the MEI formula was developed from commercial fisheries data, some conservatism may be built into it for sport fisheries.

Larkin (1978) and P. Colby (pers. comm.) have suggested that, if the fishery were to select intermediate size fish, it could maximize the yield without jeopardizing recruitment. Since angling tends to select intermediate size walleye, this may explain why yield from some of our walleye

lakes, which are primarily angling fisheries, are considerably higher than the potential estimated from the MEI formula. Table 6 compares conditions in Escanaba Lake, a small, relatively heavily angled walleye lake in northern Wisconsin, with those in Savanne Lake, a relatively unexploited lake in northern Ontario. As can be seen, there is also a marked difference in the growing day-degrees above 5C. The much higher fecundity of the walleye in Escanaba Lake may be partly a response to the higher energy input and partly a compensation for the greater fishing effort on that lake.

It is conceivable, therefore, that the guidelines for walleye (and possibly other species) could be increased for lakes where there is high energy input, efficient energy turnover and/or selection for intermediate size fish. Indeed these factors might interact to evoke a maximal compensatory response on the part of the fish populations and conceivably alter the community structure in favour of the target species. Experimental netting to determine the size and age structures of the fish populations in question would be very useful in this context. This would allow the fisheries manager to see whether the fishermen were actually selecting small to intermediate size fish or whether that was all that was available to them. However, until we acquire more information from future assessment programs and other studies, it is probably wise to be conservative in making adjustments to the recommended guidelines.

Age of fish at maturity (species and environmental differences) - It would seem reasonable to allow somewhat greater yields for fish which mature at an early age and, therefore, have a higher rate of replacement than for fish which mature later. Age to maturity will, of course, depend on species, rate of exploitation and on geographic location and environmental conditions. Smallmouth bass mature much earlier than lake trout, and lake trout in colder more northern lakes tend to mature later than lake trout towards the southern

TABLE 6. Comparison of morphometric and fishery data for a walleye lake with relatively high energy input and angling exploitation (Escanaba Lake, northern Wisconsin) with corresponding information for one with lower energy input and negligible exploitation (Savanne Lake, north-central Ontario). Some of these estimates are preliminary calculations which may be subjected to further analysis; therefore this table should not be cited for publication. Escanaba Lake data supplied by Steve Serns (pers. comm.).

Characteristics	Savanne	Escanaba
Degree-Days >5°C	1287.5	1900.8
Surface area (ha)	364.2	118.7
Shoreline length (km)	14.8	8.2
Total alkalinity (mg ℓ^{-1})	15 - 23	16
Conductivity (umhos cm^{-1})	36 - 47	46
Max. depth (m)	4.3	8
Mean depth (m)	2.57	4.3
TDS (mg ℓ^{-1})	29 - 55	25 - 43
MEI	11.3 - 21.4	5.8 - 10
Theoretical yield (kg ha^{-1})	4.17 - 5.56	3.09 - 3.94
Walleye Density (≥ Age III)	40 ha^{-1}	41 ha^{-1}
Standing crop (kg ha^{-1})	21.96 (all ages)[a]	19.1 (Ages ≥ III)
Mean # of eggs/kg body wt.	39,690	73,622
Range of # eggs/kg body wt.	29,007 - 67,125	48,441 - 74,161
Est. # eggs in pop.	83,786,000 [a]	85,892,607
Est. eggs removed (%)	9.4 [b]	7.5 [c]
Walleye fing. density (ha^{-1})	28.2 [d]	58.6 [e]
Modal size of catch (mm)	435	300

Age structure (estimated number of walleyes)

AGE		
III	4205 [a]	1846
IV	3124 [a]	1165
V	2321 [a]	840
VI	1724 [a]	442
VII	1281	192
VIII	1261	119
IX	271	92
≥X	337	197

a/ Assumed an annual percentage survival and mortality of 74.3 and 25.7, respectively for ages 1-7 and a 50-50 sex ratio for all ages.

b/ Experimental exploitation based on angling length frequencies, by removing 1.9 kg ha^{-1}.

c/ Monitoring of angling ($\bar{X}$ walleye and total species yield for 1948-75 = 9 and 19.7 kg ha^{-1} yr^{-1} respectively).

d/ Extrapolated from population estimates.

e/ Population estimates (Schnabel's method) from electrofishing, Sept. 79.

end of their distribution. This is also very apparent for walleye (Colby and Nepszy 1981). There is also some evidence that a decrease in fish densities or an increase in food supply can increase growth and delay maturity in lake trout (Martin and Fry 1973) and possibly also in some brook trout populations (D. Webster, pers. comm.).

Gear selectivity and condition of fish - Another feature to be taken into account, when applying the guidelines given in this report, is the way in which different gear may differentially select fish of the same species but in different condition. Handford *et al.* (1977) found good evidence that gill nets select out fast growing whitefish and, thus, change the rate at which a population can replace itself.

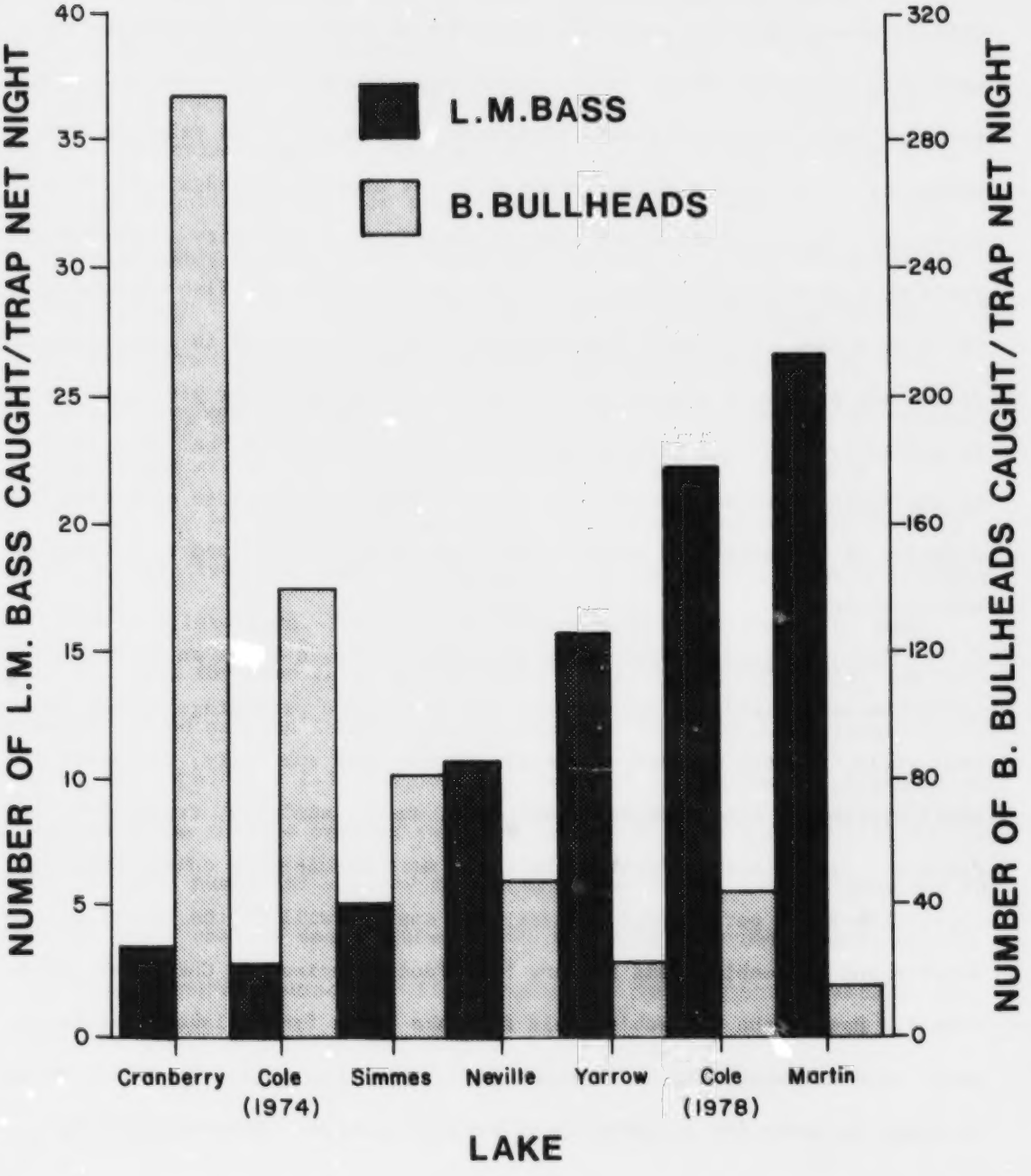
Alteration of community structure - There is much evidence that, when one species of fish is exploited to the point where its numbers are seriously reduced, another less heavily fished species may increase in number and/or size to maintain the overall yield (see SCOL Symposium). The Lake Erie fishery is a frequently cited case. If a predator is heavily exploited, its prey may exhibit increased survival. Or, if one of two species competing for a food supply is intensively fished, the other may show increased growth. Unfortunately, it is often the top quality species which are lost and smaller, less valuable species which take their place. However, numerous attempts have been made to reverse this process by intensively fishing the less desirable species. Two successful projects are cited here as examples.

Removal of 85% of the standing crop of adult white suckers from Wilson Lake in northeastern Minnesota in 1966 resulted in marked increases in abundance of yellow perch, walleye and juvenile suckers (Johnson 1977). The perch, which were not recorded in creel censuses prior to sucker removal, showed up subsequently in the sport fishery and reached a peak (0.2 kg ha^{-1}) in 1972. Before sucker removal, the average annual catch of walleye by anglers was 3.0 kg ha^{-1}, but from 1970 through 1973, they increased each year reaching 6.7 kg ha^{-1} in

1973, and averaging 4.9 kg ha^{-1}. Although evaluation of this increase in walleye catches is confounded by increased effort, attendant on improved access to the lake and publicity in a magazine, Johnson considered that they did indicate beneficial effects of removing suckers, possibly due to reduced competition for food. He concluded that, "White sucker removal may benefit percids in relatively infertile lakes of northeastern Minnesota, where the number of species present is low. In more productive waters with more diversified species composition, the productivity released by removing white suckers might be assimilated by other species that feed at the same trophic level with no measureable response by percid populations". He also noted that the average yield of walleye alone (4.9 kg ha^{-1}) was considerably greater than the potential yield for all species estimated from Ryder's MEI formula.

Sampling of six largemouth bass lakes in the Parry Sound District with trap nets indicated a reciprocal relation between numbers of largemouth bass caught per net night and numbers of brown bullheads (Thurston 1978). Since the netting on all lakes was confined to July and August each year, the differences in CUEs of the bass and bullheads apparently reflect real differences in the numbers of each species present rather than seasonal differences in behaviour and distribution of the two species. Where bullheads were most abundant, the bass were scarcest and vice versa (Fig. 5). In 1974, 1060 (135 kg) brown bullheads were removed from Cole Lake, a 32 ha lake well suited to largemouth bass, to reduce competition with, and possible predation on, the latter species. Assessment work conducted from July 1st to July 17th, 1978 revealed there was seven-fold increase in the number of adult largemouth bass (ages 2+ and older) from 1974 to 1978. Age class composition of the bass population revealed the population increase was due exclusively to the success of the 1975 year class which made up 85% of the population. The success of

Figure 5. Comparison of CUE of largemouth bass and brown bullheads in six Parry Sound District lakes. The 1974 and 1978 data for Cole Lake represent conditions prior to and following intensive netting and removal of the bullheads.


NUMBER OF L.M. BASS CAUGHT/TRAP NET NIGHT
NUMBER OF B. BULLHEADS CAUGHT/TRAP NET NIGHT
L.M.BASS
B.BULLHEADS
0
5
10
15
20
25
30
35
40
0
40
80
120
160
200
240
280
320
Cranberry
Cole (1974)
Simmes
Neville
Yarrow
Cole (1978)
Martin
LAKE

the 1975 year class was not, however, as spectacular in five other lakes studied during the summer of 1978. These five lakes were not subjected to population manipulation (bullhead removal) in 1974 and it is reasoned the substantial removal of bullheads from Cole Lake in 1974 was a major contributing factor in the exceptional success of the 1975 year class in that lake.

A review of fishery records for 43 Polish pikeperch lakes kept during 1966-71 showed that the yield was dependant on exploitation intensity and community structure (Bonar 1977). Community structure was studied on the basis of three groups of fish: predatory, undesirable, and valuable non-predatory. The percent of predatory fish was used as an index of community structure. An increase of one unit of exploitation intensity increased the yield by 0.42-0.50 kg ha^{-1} and a 1% increase in predatory fish decreased yield by 0.45-0.49 kg ha^{-1}. Undesirable fish predominated in lakes with high yields and predatory species predominated in lakes with low yields. Catches of predatory fish were highest when they comprised 25% of the total catch. On the basis of these observations, Bonar suggested that more effective regulation of predatory and nonpredatory fish might be obtained by controlled exploitation.

Species yield and community diversity - Fig. 6 shows an inverse relation between yields of lake trout, expressed as a percentage of the potential yield, and the numbers of species in the fish community, exclusive of small cyprinids, sticklebacks, mudminnows, smelt, sculpins, troutperch, and darters. It has been suggested that, the more species the energy and food supply has to be partitioned amongst, the smaller will be the potential production and allowable yield for any individual species (J. Chevalier, pers. comm.). Hence, the allowable yield for lake trout from a lake trout-smallmouth bass community may be somewhat higher than the guideline value, whereas it might be lower for a community of several species. However, such an

adjustment should be made with caution, in view of the fact that lake trout are slow to mature and exacting in water quality requirements, characteristics which make them particularly vulnerable to overexploitation.

All the lakes which Ryder used in deriving the MEI formula had relatively diversified fish communities, probably owing to the positive relation between lake size and fish diversity. As many small lakes do not have such diversified communities, one might question whether the MEI formula is applicable to such waters.

Size of lake and fish yield - Although Ryder used data from large lakes only in deriving the MEI formula, we feel it can provide a first order estimate of potential yields for small lakes. However, there seems to be a considerable number of small lakes which do not conform to the MEI model and for most of these the estimated yield appears to be low. As Ryder *et al.* pointed out, "Small lakes are exploited more efficiently per unit area than large lakes when both are subjected to proportionately similar fishing effort".

Following studies of lakes on the Manitoulin Island, the Bruce Peninsula and the La Cloche area, in which all fish species were intensively sampled, Harvey (1980 MS) found the number of species present to be positively correlated with lake area. A similar relation between the number of game species and area for some lakes in the Huronia and Lindsay Districts, the Manitoulin Island and the Toronto area can be seen in Table 7. A least squares fit gives the line: $N = 1.34 + 2.33\log_{10}A$, where N is the number of game fish species and A the surface area of the lake in ha. Here, $r = 0.780$ with 23 d.f. and $P<0.01$. The number of species in the small Manitoulin Island lakes may be limited by their shallow depth (Harvey 1980 MS) while anaerobic conditions in the hypolimnion during summer may limit the number in the kettle lakes in the Toronto area (McCombie, pers. comm.).

Figure 6. Relation between the yield of lake trout, expressed as a percentage of the potential (MEI) yield and the number of species present. The regression lines is: $Y = 74.07 - 5.14X$, where Y is the % of lake trout, X the number of species, $r = 0.66$ with 9 d.f. and $P<0.05$.

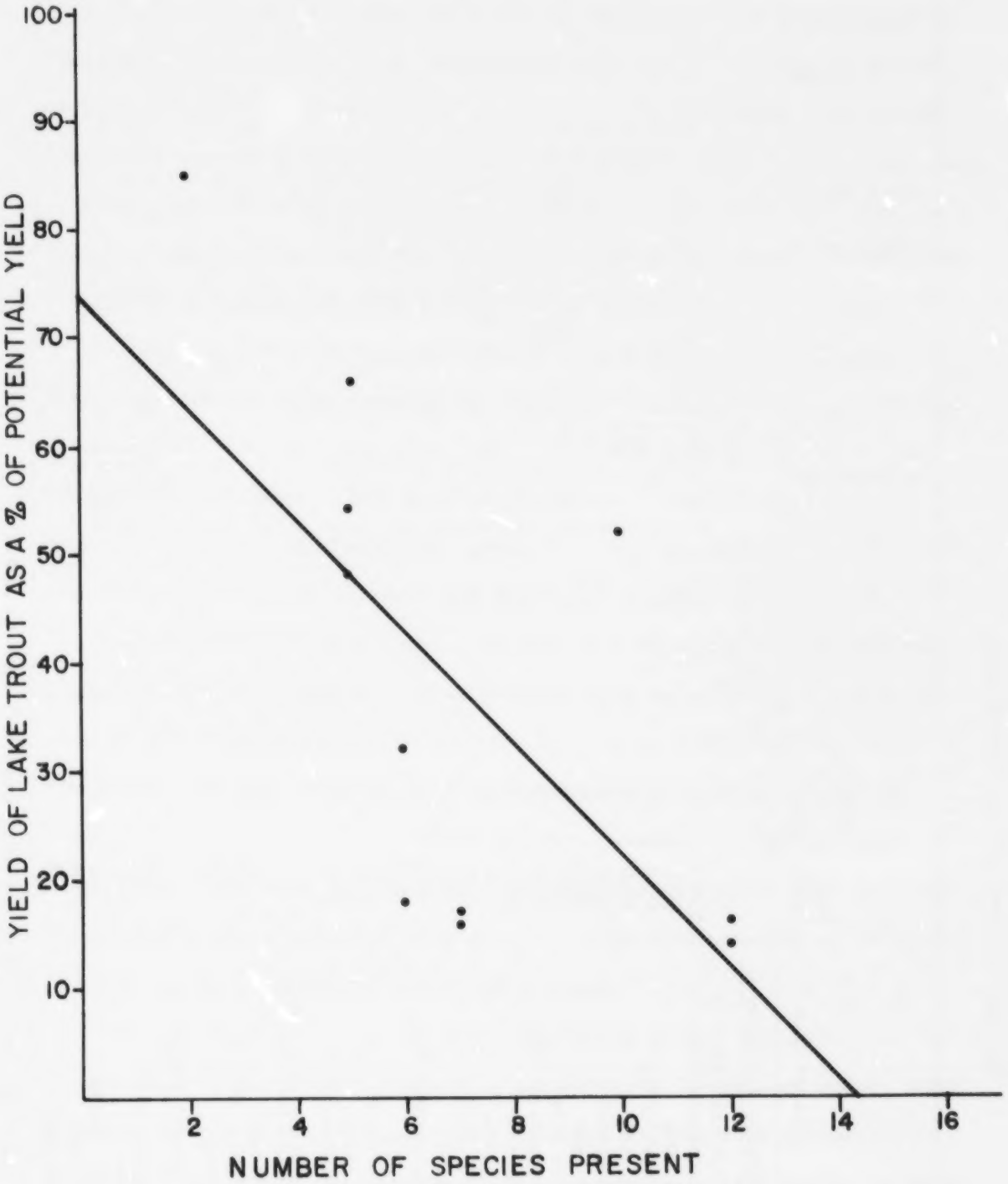

YIELD OF LAKE TROUT AS A % OF POTENTIAL YIELD
100
90
80
70
60
50
40
30
20
10
2
4
6
8
10
12
14
16
NUMBER OF SPECIES PRESENT

Table 7. Surface areas and number of game fish species present in some lakes in the Huronia and Lindsay District, the Manitoulin Island and the Toronto area.

Name of lake	Area in ha	Number of species	B. bullhead	Chan. Catfish	Burbot	Rock bass	Pumpkinseeds	Bluegill	S.M. bass	L.M. bass	Black crappie	Yellow perch	Walleye	Bowfin	Lake trout	L. whitefish	Northern pike	Muskellunge
Huronia & Lindsay D.																		
Rice Lake and Otonabeee River	10440	10	X		X	X	X	X	X	X		X	X					X
Scugog	6565	8	X			X	X		X	X		X	X					X
Couchiching	4868	13	X	X	X	X	X		X	X		X	X	X		X	X	X
Balsam	4680	9	X		X	X	X		X	X		X	X					X
Sturgeon	4300	9	X		X	X	X		X	X		X	X					X
Pigeon	3328	9	X		X	X	X		X	X		X	X					X
Six Mile	1473	9	X			X	X		X	X		X	X				X	
Gloucester Pool	1377	12	X	X		X	X	X	X	X		X	X	X			X	X
Cameron	1303	8	X			X	X		X	X		X	X					X
Sparrow	1124	11	X	X		X	X		X	X		X	X	X			X	X
St. John	618	8	X			X	X		X	X		X	X				X	
Bass	541	5				X	X		X	X		X						
Matchedash Bay	434	9	X				X	X	X	X		X	X	X			X	
Orr	303	7	X			X	X		X	X		X					X	
Morrison	246	5					X		X	X		X						X
Little	228	7	X			X	X			X		X	X				X	
Midland Park	145	7	X			X	X	X	X	X		X						
Manitoulin Island																		
Wickett	42	2										X					X	
Smoky Hollow	28	2										X					X	
Hogg	18	4				X	X					X					X	
Toronto Area																		
Eaton Hall	18	6	X				X	X	X	X		X						
Mary	14	7				X	X			X		X					X	
St. George	10	7	X			X	X	X		X			X				X	
Simeon	6	2	X				X											
Thompson	4	1	X															

Game spp. only: Carp, suckers, and small spp. excluded.
Wanderers from Lake Simcoe.

Effect of fish stocking on yields - Maintenance stockings of fish in a lake can invalidate the potential yield estimated from the MEI because the model was derived from naturally reproducing populations. Hatchery reared fish, or fish transferred from other waters, may have put on a considerable fraction of their growth in an environment which has no relation to the MEI of the stocked lake. Although the presence of such fish might increase the fishermens' catch it would not increase the potential yield. While the growth of these fish following planting will depend on the available food supply, which in turn depends on the MEI, the numbers caught are probably more closely related to the numbers stocked and the effort expended to catch them.

Cultural eutrophication and the MEI - At present, it is not known to what extent the MEI, and consequently potential fish yields, may be affected by phosphorus, nitrogen, and other plant nutrients contributed to the lake by agricultural, urban and/or cottage development. This problem is being examined as part of the Lakeshore Capacity Study. Conceivably, these nutrients could have both deleterious and beneficial results.

However, if the additional nutrients were to stimulate blooms of phytoplankton and, if on dying and being decomposed by bacteria these blooms were to lower the dissolved oxygen of the hypolimnion to a critical level (say <5 mg l^{-1}), the lake would be rendered unsuitable to species such as lake trout, which seek the deeper, cooler strata in summer. In shallow lakes cultural eutrophication may increase the incidence of winterkill. Lowering the allowable yield to assure escapement of sufficient spawning stock would probably not help much under these circumstances.

Alternatively, if the increased production of phytoplankton were to be exploited by the zooplankton and/or bottom fauna, energy and matter might be passed up the food chain and lead ultimately to increased production of game fish. The practice of adding organic or inorganic fertilizers to ponds

to enhance production of carp and other warm water species has a long history in Europe and the Orient, but attempts in increase production of trout in Canadian waters has met with variable success (Langford 1948; Smith 1954). Reports from British Columbia and the State of Washington of increased salmon production in recent years, as a result of intentional or unintentional enrichment of lake waters, have been reviewed by Stockner (1979). However, he cautions, "For a variety of reasons ..., treated lakes responded differently to fertilization, suggesting that extrapolation of results.... could be erroneous and/or dangerous". Therefore, it is not clear at present whether the production of Ontario game and commercial fish would be sufficiently enhanced by cultural eutrophication to affect the guidelines for allowable catches recommended here. It is probably advisable to be cautious in the face of inadequate information.

Acid precipitation and fish yields - There is no doubt that acid precipitation can drastically reduce production and catches of fish in oligotrophic lakes which have characteristically low buffering capacity. The effects are manifold, sometimes very subtle and often not well understood. Among the possible direct effects on fish are decreased fecundity, impaired hatching and increased post hatching mortality. There can also be indirect effects through reduction of zooplankton and bottom fauna which serve as food for fish.

Recent studies on some lakes in the Muskoka-Haliburton area have shown that increased mobilization of cations in acid stressed situations can increase the specific conductance readings (Dillon *et al.* 1980). This in turn can lead to elevated total dissolved solids values, since these are usually derived from a regression of TDS on conductance. Under these circumstances, the MEI ($= TDS/\bar{Z}$) and fish yields predicted therefrom could be inflated by the presence of ions which play only a minor role in biological production. Hence, allowable yields for lakes known to be vulnerable to acid precipitation should probably be conservative, to compensate for possible losses of fish and over-

estimation of potential yields. This would, of course, only delay the impact of acidification rather than avert it.

CONCLUSION

Since the guidelines proposed here are based on long-term records, in many instances, for fisheries which have withstood moderate to heavy fishing pressure, they should provide reasonable first approximations for quotas to protect existing spawning stocks and community structures. However, once these guidelines are applied, they should certainly be tested and adjusted as Assessment Units and Districts monitor the fisheries. Information gathered by the Assessment Units and other biological agencies will lead to a better understanding of the problems discussed above under qualifications. This information will also help in the development of more rigorous models for predicting potential or sustainable yields. At present, significant advances are being made in our Fisheries Research Section and by the University of Toronto towards dealing with the energy factor. The role of phosphorus in fish yields from Ontario lakes is being explored in the Lakeshore Capacity Study and a detailed model, relating the successive links in the aquatic food chain and the various components of the aquatic plant and animal communities, is being developed at the University of Toronto.

Among the features of fisheries to be monitored, with a view to testing and improving the guidelines, are: (1) total catches and yields for individual species and for the whole fish community; (2) species composition and diversity of fish populations; (3) age and size composition of fishermen's catches and of the fish populations; (4) angling and/or commercial fishing effort; (5) rate of growth and age at maturity for the various species caught; and (6) rates of total, natural and fishing mortality. The information on fishermen's catches

will come from creel censuses, commercial fish landing reports, and sampling of commercial catches by MNR personnel. Data on fish populations will be obtained by experimental netting by Assessment Unit and other MNR personnel.

The collection of effort statistics for sport fisheries is usually an integral part of any creel census. However, it may be desirable to adopt a standard unit of effort, such as the angler-hour or rod-hour, and to devise more rigorous and standardized sampling designs for the collection of statistics in the future. There is also a real need to decide on a standard unit of commercial fishing effort, such as the net-night or yard-night, and to find some procedure for collecting this information. Eventually too, some factors or formulae should be developed to modify both sport and commercial fishing effort so as to take account of the fact that a unit of effort with different gear may select quite different sizes, ages or even species of fish and ultimately produce quite different yields.

If these features remain more or less constant from year to year, this may be taken as an indication that the guidelines are satisfactory. On the other hand, a decline in the proportion of preferred fish species or a decrease in the average age of fish in the population, to the point where it coincides with the average age at maturity, would suggest that the guidelines were not stringent enough for the fishery in question. Increases in fishing effort or changes in selectivity, when accompanied by undesirable changes in species composition and/or loss of spawning stocks, would indicate the need to reduce the guideline values. In some instances, a decrease in average age and size of fish caught might be considered to be a loss in quality of the fishery, quite apart from a loss of potential spawning stocks.

For some percid fisheries, and perhaps in other instances where demand for fishing opportunities is high, one might relax the guidelines to begin with and then tighten them, should subsequent monitoring indicate undesirable results. However, it should be borne in mind that it may be very difficult,

or even impossible, to restore a fishery if it is allowed to deteriorate too far.

As has been shown above, considerable progress has been made recently in mathematically modelling the effect on fish yields of MEI and effort combined and of MEI and energy input combined. What is needed now is a model (regression equation) combining all three factors, MEI, effort and energy input, for a representative set of widely distributed Ontario lakes. Whether separate regression lines are needed for different fish communities or different lake types (nutrient and energy sinks versus those with efficient recycling) should also be investigated further. Hopefully the data generated by the Assessment Units and other OMNR fisheries components in the next few years will provide the information required for this modelling.

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GLOSSARY

allowable yield - A prescribed yield level in kg $ha^{-1}yr^{-1}$.

compensatory reserve - The ability of fish communities or populations to sustain a fishery without collapsing. It involves physiological, behavioural and genetic compensating responses to selective removal of components of the fish population (Regier and Loftus 1972). Abrosov (1969) considered compensatory reserve in his approach to fish management.

effort - The form and intensity of fishing activity. Though most often expressed as rod-hours, net yardage or some comparable term *effort* also entails vessel capabilities, gear type (efficiency, selectivity, specificity), the application of skills and knowledge, and to the time and place the activity is carried out.

fishing pressure - A measure of the stress induced by a fishery on a fish stock or fish community. It is equivalent to the term *intensity of fishing* used by Ricker (1977) and *effort* used by Rothschild (1977). These authors agree that the instantaneous rate of fishing is a measure of *pressure*.

harvest - The total quantity of fish (landed catch) removed by fishermen from an ecosystem or fish community.

potential yield - In the context of Ryder (1965), it is the theoretical maximum yield that can be taken annually without exhausting the compensatory reserve of a fish community. It is analogous to maximum sustainable yield, maximum equilibrium yield and theoretical yield.

yield - Rate of harvest given on a per unit area and season basis, usually expressed in kg $ha^{-1}yr^{-1}$.

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APPENDIX 1[1]

SCIENTIFIC NAMES OF FISH

Lake herring	*Coregonus artedii*
Lake whitefish	*Coregonus clupeaformis*
Rainbow trout	*Salmo gairdneri*
Landlocked salmon	*Salmo salar*
Brook trout	*Salvelinus fontinalis*
Lake trout	*Salvelinus namaycush*
Northern pike	*Esox lucius*
Muskellunge	*Esox masquinongy*
White sucker	*Catostomus commersoni*
Brown bullhead	*Ictalurus nebulosus*
Smallmouth bass	*Micropterus dolomieui*
Largemouth bass	*Micropterus salmoides*
Yellow perch	*Perca flavescens*
Walleye	*Stizostedion vitreum vitreum*

[1]Scientific names conform to those in American Fisheries Society Special Publication No. 12. 1980. A list of common and scientific names of fishes from the United States and Canada (Fourth Edition).

APPENDIX 2

STANDARDIZATION OF THE TDS DATA

The total dissolved solids data used in this report to calculate the MEI values and ultimately the potential yields were drawn from various sources. While a few were taken from published literature, the majority came from file reports on MNR creel censuses and were originally obtained in the lake survey program. However, since it was not always clearly stated at what time of year the water sampling was done and, since the MNR Aquatic Habitat Inventory has recently revised the formula for converting specific conductance to TDS, we have attempted to standardize the data more rigorously in this version of the report.

A list of lakes concerned was forwarded to Gareth Goodchild of Fisheries Branch together with a request for all related specific conductance and cell temperature data on file and the new formula for converting to TDS. His co-operation is gratefully acknowledged. On receiving the conductance data we first standardized them to 25C using the usual formula: $COND_{25} = COND_t / (1+(0.02(t-25)))$; where $COND_{25}$ is the specific conductance at 25C in μmhos cm^{-1} and $COND_t$ is the specific conductance at the temperature, t, at which the original reading was made (= the cell temperature). For most of the lakes more than one conductance reading was available, in which case the lowest summer reading was selected for conversion to TDS, to conform to the constraint suggested by Ryder (1964). Conversion to TDS was done with the new formula: $TDS = 0.666COND_{25}$ rather than the former one: $TDS = 0.6353COND_{25} + 10.2$, which was used in preparing the conversion chart in the Aquatic Habitat Inventory Surveys Manual. It should be noted that the error in determining a TDS value is about 15%.

In the few cases where the TDS data were taken from the literature, or where only TDS values were available from MNR sources, the data were taken as reported. Note that there is no need to change the TDS data used in fitting the Ryder line: $Y = 1.4\ (TDS/\text{mean depth})^{0.45}$ because the TDS values he used were determined gravimetrically.

As a result of selecting the lowest specific conductance readings and applying the new conversion factor, some of the TDS, MEI and potential yield data in this report differ from those in the previous version. In general, values at the lower end of the scale were increased while those towards the upper end decreased. However, these effects seem to have cancelled out so that the guidelines for species yields recommended in this report are not appreciably different from those in the previous one.

The fact that, in spite of the revisions in TDS values made in the present report the recommended species yield guidelines are not significantly different from those in the earlier version, should not be construed to mean that any measure of specific conductance or TDS is satisfactory for estimating potential fish yields. On the contrary, if one plots the Ryder curve: $Y = 1.4(MEI)^{0.45}$ on arithmetic scales, it becomes obvious that a slight difference in MEI for a lake towards the lower end of the MEI range can cause a marked difference in the estimate of potential yield. Hence more care should be taken in future in reporting where, when and at what depth the specific conductances were taken and how the conversion to TDS values was made. This applies particularly to creel census reports in which the TDS data are quoted second hand. An updating of some of the earlier lake surveys is also desirable.

APPENDIX 3

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